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Among the marine planktonic Crustacea, the amphipods frequently play an important role in the economy of the sea. In general they rank third in numerical abundance; they are far exceeded by the copepods and euphausiids. In tropical and subtropical regions pelagic amphipods are not usually found in large numbers, but in the cooler parts of the oceans they are often extremely abundant. Members of the genus *Parathemisto* (=*Themisto* auct.) overwhelmingly dominate the cool-water epipelagic amphipod fauna, and their importance in the north Atlantic (including the Arctic Atlantic) has been pointed out by Bigelow (1926), Bigelow and Sears (1939), Stephensen (1923, 1924), and Dunbar (1946, 1957). Only cursory attention has been given to north Pacific representatives. The present paper is an attempt to fill in a few gaps in our knowledge of the distribution and life history of species of *Parathemisto* in the north Pacific and the Arctic Ocean north of Alaska and western Canada.

The amphipods upon which this report is based were obtained from plankton collections from several sources: (1) Off the Pacific coast of the United States from the latitude of the Columbia River to that of Punta Eugenia in middle Baja California, in connection with the California Cooperative Oceanic Fisheries Investigation (CCOFI). (2)

The *Northern Holiday* Expedition of the Scripps Institution of Oceanography, August and September 1951. (3) Cruises of the United States Fisheries steamer *Albatross* in the northern Pacific. (4) Cruises of the U.S.S. *Burton Island* to the Chukchi and Beaufort Seas during August 1950 and August and September 1951, and to Amundsen Gulf and Prince of Wales Strait during August 1953. (5) Northern Pacific stations of cruise VII of the *Carnegie*, 1928–29. (6) Samples from Japanese waters, sent to me by Dr. Sigeru Motoda and Mr. Zinziro Nakai. (7) Samples from Korean waters provided by Mr. Won Tack Yang.

Five species of *Parathemisto* were obtained from these collections. Each species is considered separately below with respect to its taxonomy, distribution, and ecology. A sixth species, doubtfully identified from the Yellow Sea by Yamada, is also considered.

Much of the work reported herein was carried out under the supervision of Dr. Martin W. Johnson, Scripps Institution of Oceanography, to whom I am grateful for many valuable suggestions and for forwarding to me the amphipods from the 1951 *Burton Island* Cruise. Dr. Robert Bieri, Antioch College, kindly sent me the amphipods from the 1953 *Burton Island* Cruise. I also wish to thank Dr. Sigeru Motoda, Hokkaido University, and Mr. Zinziro Nakai, Tokai Regional Research Laboratory, for sending me specimens of *Parathemisto* from Japanese waters. Mr. Won Tack Yang, Central Fisheries Experiment Station, Pusan, obligingly sent me specimens from several localities around Korea. Dr. Isabella Gordon, British Museum (Natural History), made it possible for me to examine *Challenger* specimens of *Parathemisto pacifica* Stebbing.

Genus *Parathemisto* Boeck

Themisto Guérin, 1825, p. 772.—Stephensen, 1923, p. 19; 1924, p. 94.
Parathemisto Boeck, 1870, p. 87.—Bovallius, 1889, p. 248.—Barnard, 1930, p. 419.
Euthemisto Bovallius, 1887, p. 21; 1889, p. 275.

DIAGNOSIS (FAMILY CHARACTERS OMITTED): Head moderately large, globular. P1 (pereopod 1) simple. P2 chelate; carpal process narrow, concave on anterior margin. Carpus of P3 and P4 more or less dilated, forming a prehensile organ with propodus. P5–7 longer than P3 and P4. Uropods narrow, elongate. Type species, by monotypy, *Themisto gaudichaudii* Guérin.

In 1870 Boeck established the genus *Parathemisto*, which was to be distinguished from *Themisto* Guérin by P5 not being much longer than P6 or P7. Noting that *Themisto* had been preoccupied in 1815 by a nudibranch mollusk, Bovallius (1887) changed the amphipod name to *Euthemisto*. Stephensen (1924) combined the two genera, since the relative lengths of P5–7 of the male of *Themisto gracilipes* Norman

placed it in *Euthemisto*, while the female had to be referred to *Parathemisto*. In combining the two genera, Stephensen returned to the oldest generic name, apparently not realizing that it had been preoccupied. K. H. Barnard (1930) pointed out that *Themisto* was not available and that Boeck's name had to be used. In spite of this, some authors continue to refer to the genus as *Themisto*.

K. H. Barnard (1930) retains *Parathemisto* and *Euthemisto* as subgenera of *Parathemisto*, a course which is followed by Hurley (1955) and Vinogradov (1956). I believe this is the most satisfactory way to deal with this group of amphipods. Although the differences between *Euthemisto* and *Parathemisto* are sufficiently clear cut so that there is no difficulty in assigning all the known species to one or the other, they are not as great as those which separate the other genera of the family Hyperiidae.

Keys to species of *Parathemisto* have been given by Barnard (1930, p. 420), Stephensen (1923, p. 19, European species), and Hurley (1955, New Zealand species).

Subgenus *Parathemisto* Boeck

Dorsal spines absent. Flagellum of female antenna 1 slender, straight. Carpus of P3–4 only slightly expanded. P5–7 subequal in length. Peduncle of uropod 3 strongly produced at inner distal angle. Inner ramus of uropod 3 serrate on medial and lateral margins. Type species, by subsequent designation, *Parathemisto abyssorum* Boeck.

Key to the Species of the Subgenus *Parathemisto*

1. In length P5>P7>P6; dactyls not pectinate. Posterior margin of P1 propodus bearing several long setae. Maxilliped without a distal row of setae on basal plate . . . . . **abyssorum** Boeck
   In length P6>P7>P5; dactyls of P5–6 pectinate at base. Posterior margin of P1 propodus serrate but without setae on distal margin. Maxilliped with distal row of long setae on basal plate 2
2. Antennae 1 and 2 of female subequal. Length of adult 4.5–8.5 mm. **pacifica** Stebbing
   Antenna 2 longer than antenna 1. Length of adult 9–17 mm. **japonica** Bovallius

Parathemisto (Parathemisto) pacifica Stebbing

FIGURES 1; 2,*a*,*j*–*k*; 3,*a*–*e*; 4–10

Parathemisto pacifica Stebbing, 1888, pp, 1420–1423 [no figures].—Bovallius, 1889, p. 263.
Parathemisto oblivia (Krøyer), Holmes, 1904, p. 233.
Themisto abyssorum (Boeck), Shoemaker, 1930, pp. 132–133 [specimens from Nanaimo, British Columbia only].—Wailes, 1929, p. 5.

Parathemisto abyssorum (Boeck), Thorsteinson, 1941, pp. 90–91.
Parathemisto japonica Bovallius, Hurley, 1956, pp. 15–16.—Vinogradov, 1956, pp. 211–212.

DIAGNOSIS: Total length of adult ♀, excluding antennae, 4.5–8.5 mm. Body more chunky in appearance than in most species of *Parathemisto*. Dorsal to antennal groove head is less roundly produced in lateral view than in *P. abyssorum*, i.e., slope of this part of head is directed more posteriad than in *P. abyssorum*. Pleonites with a few minute teeth along ventral margins, posterior lateral corners produced into small points. Female antenna 2 about as long as antenna 1, slightly shorter than head plus first 2 pereonites. Molar process of mandible about twice as long as incisor process. Maxilliped with row of long spines at distal end of basal plate. Propodus of P1 serrate but not spinous on posterior margin. In length P6>P7>P5. Posterior distal corners of carpus of P6–7, but not of P5, with conspicuous spines. Dactyls of P5–6 pectinate at base. Peduncle of uropod 3 from 2 to 2.5 times as long as telson.

REMARKS: K. H. Barnard (1930, p. 419) suggested that Stebbing's *P. pacifica* was a synonym of *P. japonica*. Barnard did not have specimens of either species, and his conclusion was a reasonable one to draw from a comparison of the descriptions by Bovallius and Stebbing. I suspect that Stebbing would have reached the same conclusion, for at the time he described *P. pacifica*, Bovallius had published only a brief, unillustrated description of *P. japonica*. If Bovallius' more detailed and illustrated description published in 1889 had been available to Stebbing, he might not have described *P. pacifica* as a separate species, for the differences emphasized by Stebbing and listed below are actually not valid for distinguishing the two species:

1. The propodus of P3 of *P. pacifica* is longer than the carpus and is pectinate rather than smooth on the posterior margin. While Bovallius (1889) states that the propodus is a little shorter than the carpus, he also says that the propodus is finely pectinated, and in his figure 35, plate 12, it is shown as pectinate and slightly longer than the carpus.

2. In *P. pacifica*, the outer ramus of uropod 3 is shorter than the inner ramus. Although Bovallius (1889) states that the two rami are of equal length in *P. japonica*, his figure 43, plate 12, shows the outer one to be slightly shorter. Stebbing does not say how much shorter the outer ramus of *P. pacifica* is, and provides no figures. In my specimens of *P. japonica* and *P. pacifica*, the outer ramus is slightly shorter.

Although the above criteria are worthless for distinguishing between *P. pacifica* and *P. japonica*, I nevertheless consider them as distinct

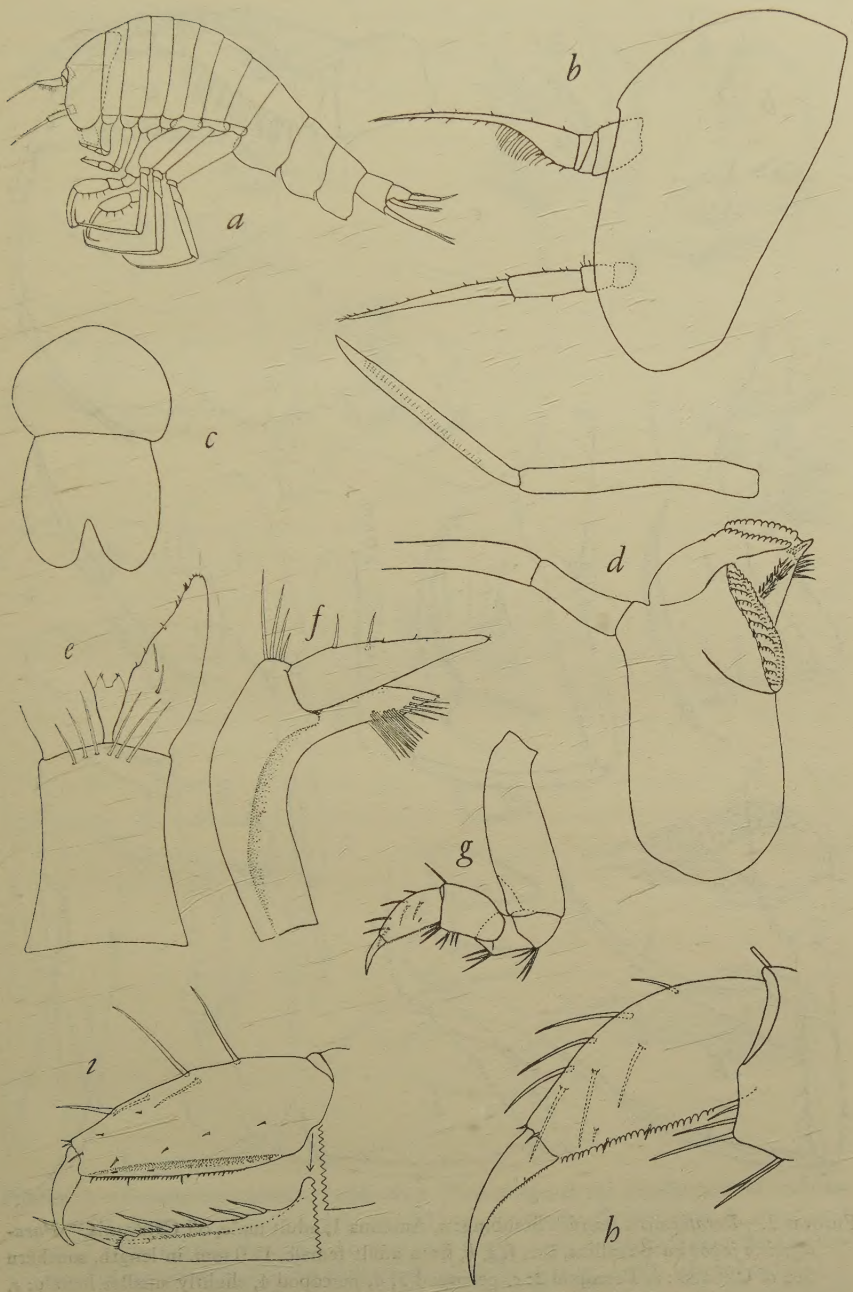

FIGURE 1.—*Parathemisto pacifica* Stebbing: *a*, Lateral view of female, 5.0 mm. in length; *b*, head and antennae, lateral view; *c*, labrum, male; *d*, left mandible, male; *e*, maxilliped, posterior surface; *f*, maxilliped, lateral view; *g*, *h*, pereopod 1, female; *i*, pereopod 2, female. Scales various.

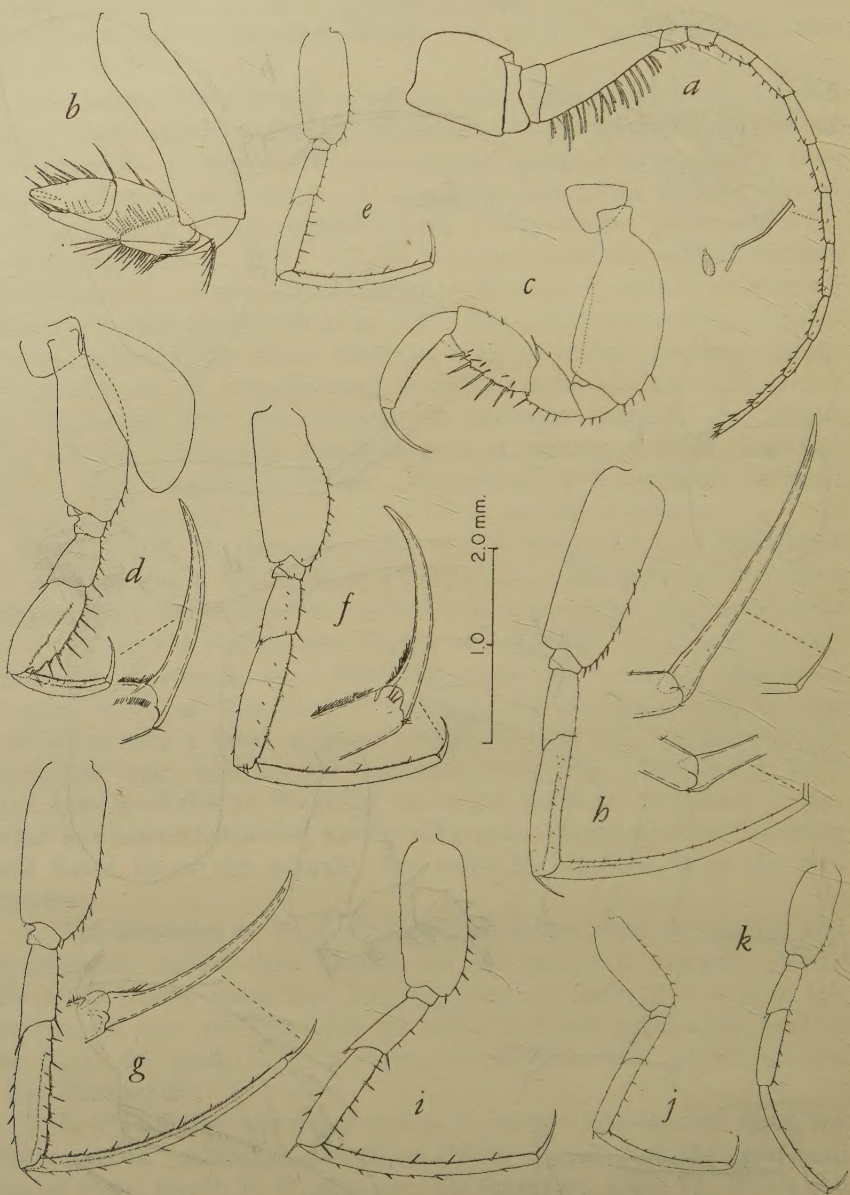

FIGURE 2.—*Parathemisto pacifica* Stebbing: *a*, Antenna 1, adult male, off California. *Parathemisto japonica* Bovallius, *b*, *c*, *f*, *g*, *h*, from adult female, 11.0 mm. in length, southern Sea of Okhotsk: *b*, Pereopod 2; *c*, pereopod 3; *d*, pereopod 4, slightly smaller female; *e*, pereopod 6, juvenile female, 6.7 mm., off Cape Esan, Japan; *f*, pereopod 5; *g*, pereopod 6; *h*, pereopod 7, dactyl broken, undamaged dactyl drawn from slightly smaller specimen, same locality; *i*, pereopod 6, ovigerous female, 9.5 mm., off Cape Esan. *Parathemisto pacifica* Stebbing, pereopod 6: *j*, Ovigerous female, 7.0 mm., off Cape Esan; *k*, adolescent female, 6.7 mm., Bering Sea. Scale same for *c*-*k*; enlargement 3.8 times greater in *a*, and 1.5 times greater in *b*.

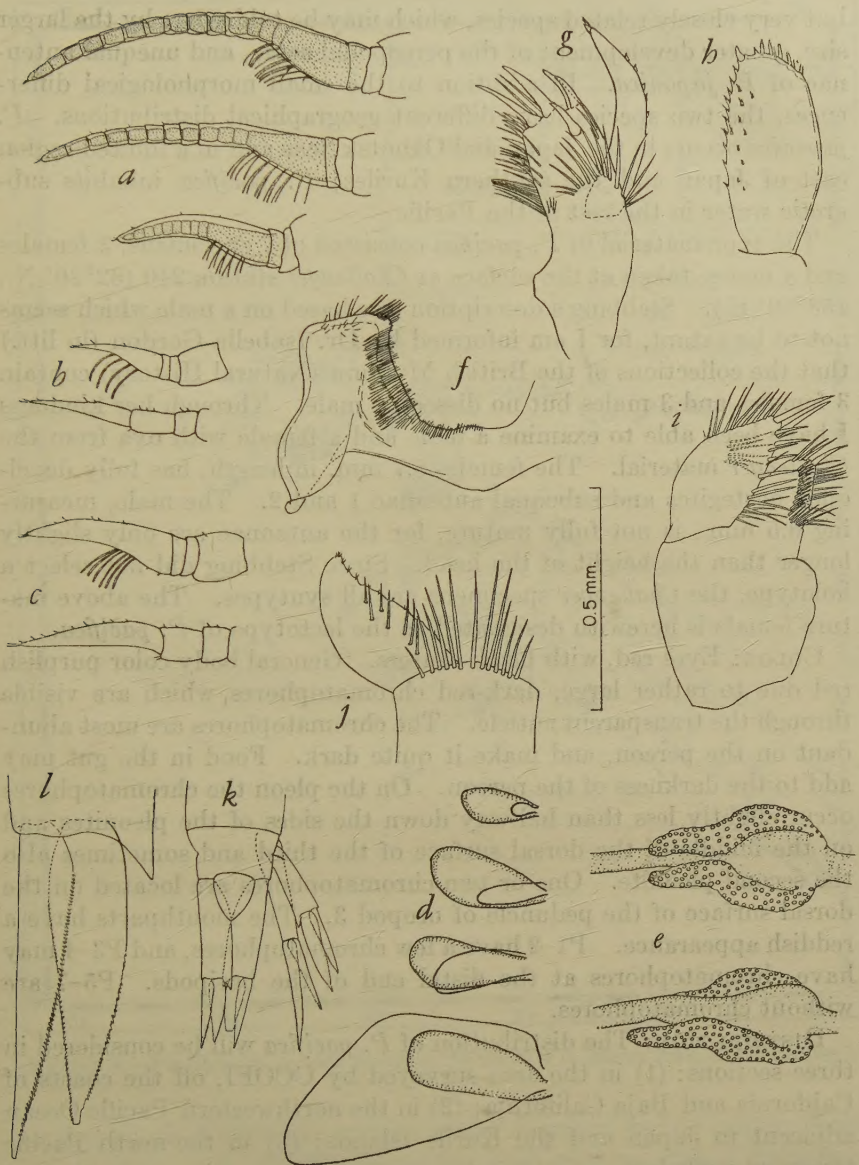

FIGURE 3.—*Parathemisto pacifica* Stebbing: *a*, Three stages in the development of male antenna 1, from specimens 3.8, 4.5, and 5.0 mm. in length, off California; *b*, antennae 1 and 2 of very young female; *c*, same of very young male; *d*, four stages in the development of oostegites (unshaded outline) showing size relative to gills (shaded outline); *e*, dorsal (above) and dorsolateral views of portion of digestive system, showing origin of digestive caecae from anterior part of midgut. *Parathemisto japonica* Bovallius: *f*, Labium; *g*, maxilla 1; *h*, palp of maxilla 1, flattened; *i*, maxilla 2; *j*, maxilliped, inner plate and left outer plate omitted; *k*, uropods and telson; *l*, uropod 3, distal end. Scale applies to *f–j*.

but very closely related species, which may be told apart by the larger size, greater development of the pereopodal setae, and unequal antennae of *P. japonica*. In addition to the small morphological differences, the two species have different geographical distributions. *P. japonica* occurs in the Japan and Okhotsk Seas and in a limited region east of Japan and the southern Kuriles; *P. pacifica* inhabits subarctic water in the rest of the Pacific.

The type material of *P. pacifica* consisted of 7 specimens, 3 females and 4 males, taken at the surface at *Challenger* station 240 (32°20′ N., 153°39′ E.). Stebbing's description was based on a male which seems not to be extant, for I am informed by Dr. Isabella Gordon (in litt.) that the collections of the British Museum (Natural History) contain 3 females and 3 males but no dissected male. Through her kindness I have been able to examine a male and a female with ova from the *Challenger* material. The female, 6.7 mm. in length, has fully developed oostegites and subequal antennae 1 and 2. The male, measuring 6.5 mm., is not fully mature, for the antennae are only slightly longer than the height of the head. Since Stebbing did not select a holotype, the *Challenger* specimens are all syntypes. The above mature female is herewith designated as the lectotype of *P. pacifica*.

Color: Eyes red, with black centers. General body color purplish red due to rather large, dark-red chromatophores, which are visible through the transparent cuticle. The chromatophores are most abundant on the pereon, and make it quite dark. Food in the gut may add to the darkness of the pereon. On the pleon the chromatophores occur slightly less than halfway down the sides of the pleonites and on the middle of the dorsal surface of the third and sometimes also the second pleonite. One or two chromatophores are located on the dorsal surface of the peduncle of uropod 3. The mouthparts have a reddish appearance. P1–2 have a few chromatophores, and P3–4 may have chromatophores at the distal end of the basipods. P5–7 are without chromatophores.

Distribution: The distribution of *P. pacifica* will be considered in three sections: (1) in the area surveyed by CCOFI, off the coasts of California and Baja California; (2) in the northwestern Pacific Ocean adjacent to Japan and the Kurile Islands; (3) in the north Pacific Ocean as a whole.

1. CCOFI Area: Figures 4 to 7 show the distribution of *P. pacifica* encountered during four CCOFI cruises. At the stations shown, oblique hauls of 20 minutes duration were made with one-meter plankton nets from a depth of about 70 m. (140 m. in cruise 20 except for the northernmost line of stations) to the surface. Details of net construction and methods by which the hauls were made are given by Ahlstrom (1948, 1952). The volume of water strained during a haul was meas-

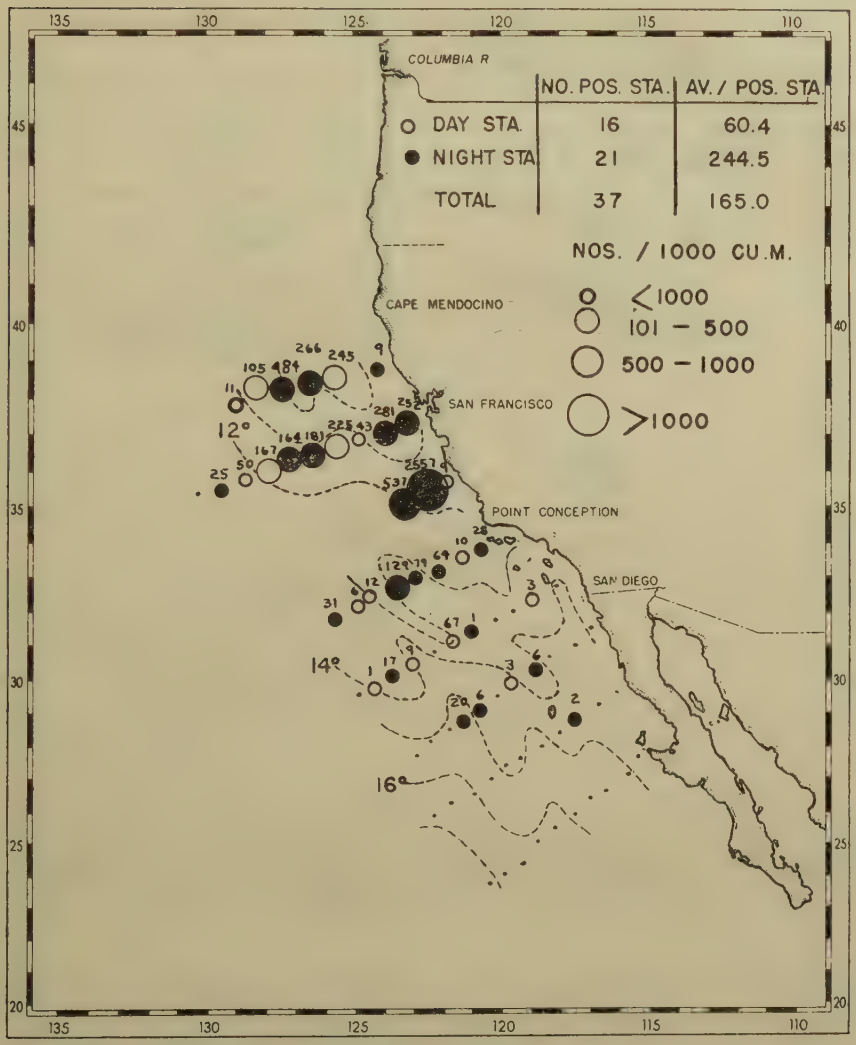

FIGURE 4.—*Parathemisto pacifica* Stebbing, distribution in March 1949, CCOFI cruise 1.

ured with an Atlas-type current meter fastened in the center of the mouth of the net. This measure has been used to correct the counts of the numbers of amphipods in the samples studied to numbers per 1,000 cubic m. of water.

In the CCOFI area *P. pacifica* is by far the most abundant amphipod. The southern extent of its range lies within the CCOFI area, and by comparing the southern boundaries with the superimposed isotherms at a depth of 30 m., it is possible to estimate the limiting temperatures. In cruise 1 this temperature is estimated to be about

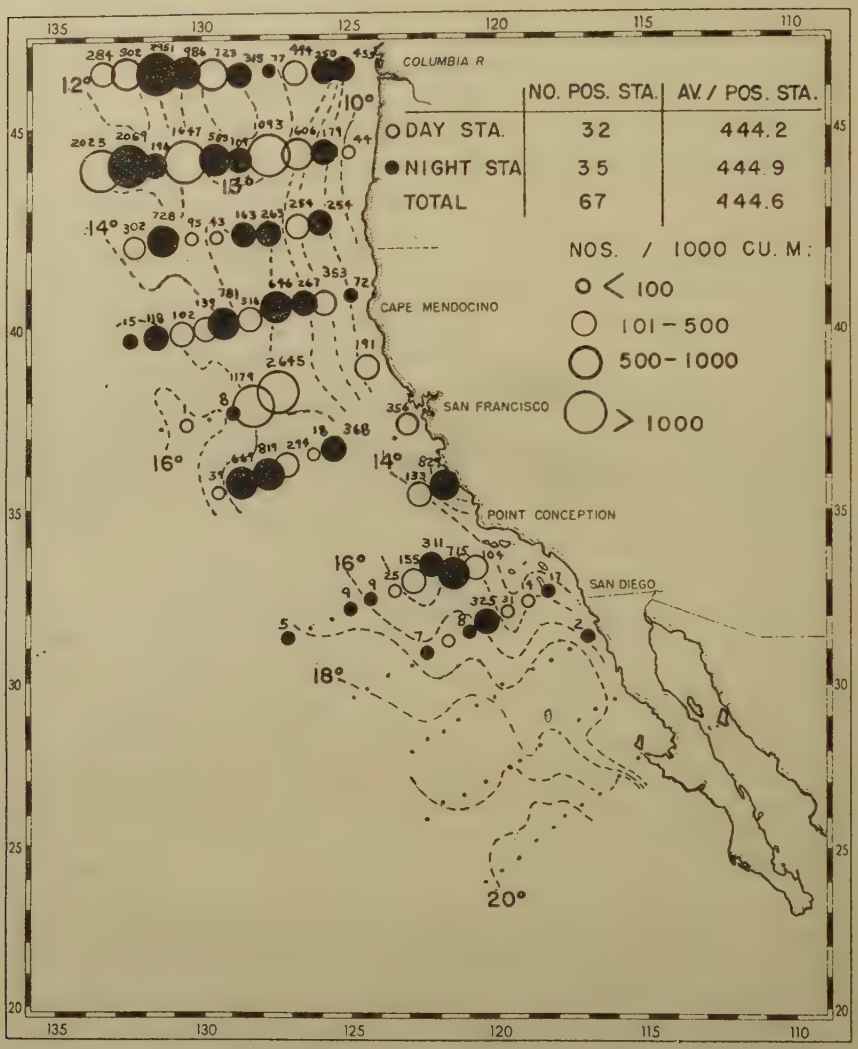

FIGURE 5.—*Parathemisto pacifica* Stebbing, distribution in July 1949, CCOFI cruise 5.

15° C., and for cruises 5 and 9 about 17°. The data of cruise 20 are very limited, but here the 18° isotherm may be limiting.

The numbers found at the different stations of a cruise vary considerably. Near the southern limits the numbers decrease somewhat, but elsewhere the variation appears to be random and not related to available measurements of oceanographic conditions. An unsuccessful attempt was made to determine the causes behind this variation in numbers in cruise 5. Using the northern four lines of stations in order to eliminate the limiting effect of higher temperatures to the

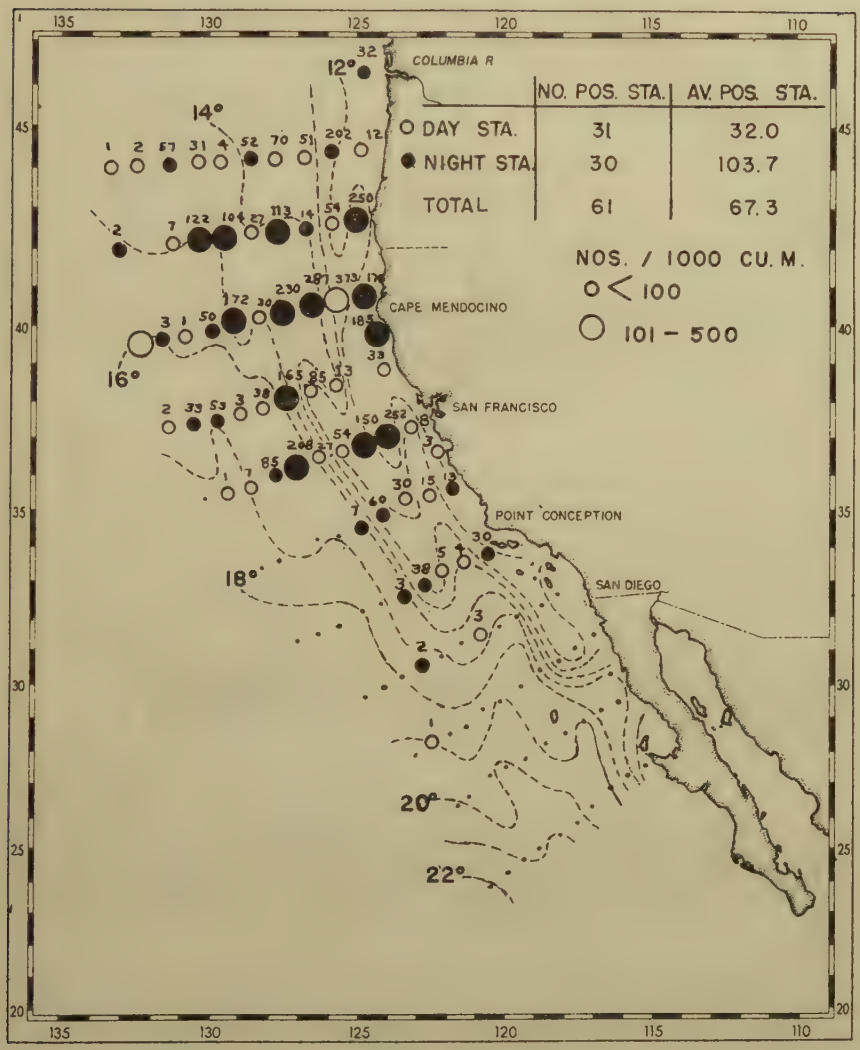

FIGURE 6.—*Parathemisto pacifica* Stebbing, distribution in November 1949, CCOFI cruise 9.

south, it was not possible to find any relation between the numbers taken at a station and the temperature, salinity, depth of haul, depth of thermocline, or the percent of the haul which was made below the thermocline.

The seasonal variation in numbers is of considerable interest. The average number per 1,000 cubic m. at the positive stations in 1949 increased from 165 in March to 445 in July, and then decreased to only 67 in November. Part of the March–July increase may be at-

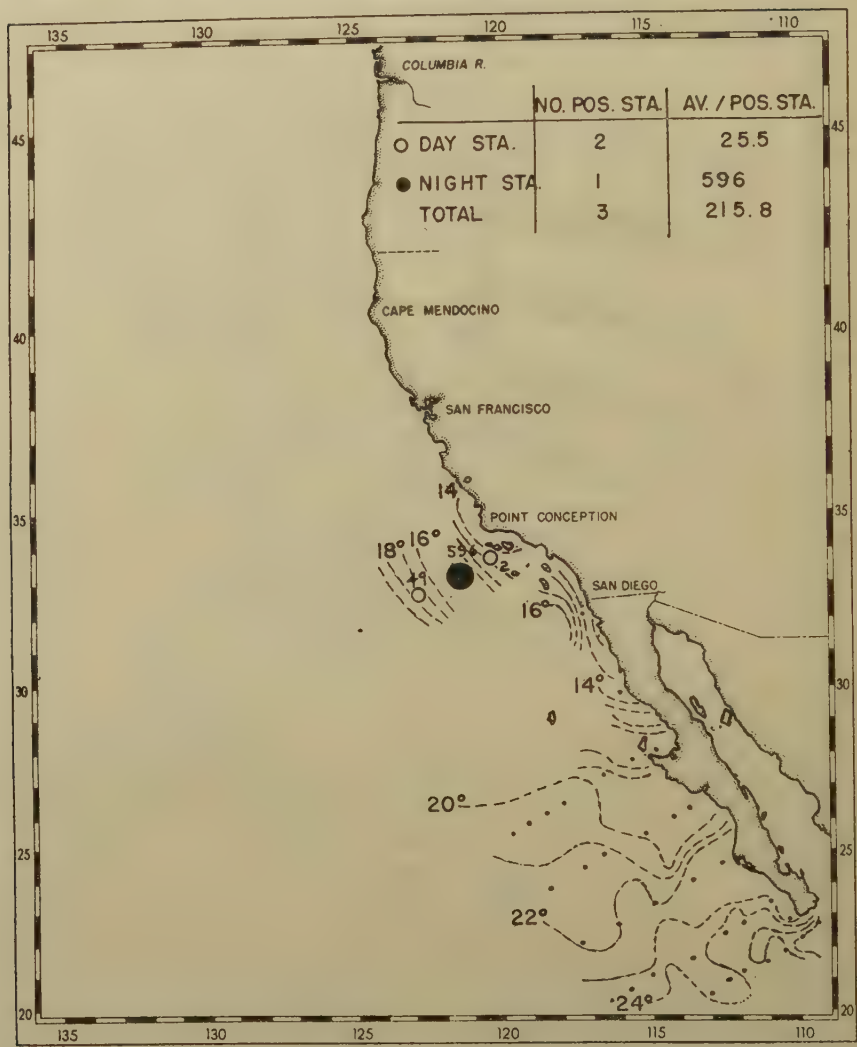

FIGURE 7.—*Parathemisto pacifica* Stebbing, distribution in November 1950, CCOFI cruise 20.

tributed to the fact that in March the four northernmost lines of stations were not occupied, and the average number is more heavily affected by the small numbers in the southernmost lines. But even if we consider only lines 5–8 of cruise 1, the mean number per station is increased only to 229, which still falls far short of the mean number for July, 445, or the mean number for lines 5–8 in July, 404. In November not only is there a notable decrease in numbers, but the range is slightly more restricted because of the higher temperatures of offshore waters.

Part of the variation in numbers may be caused by seasonal changes in the intensity of breeding. However, females with ova or embryos in the brood pouch were abundant at all but the southernmost stations on all three cruises. Juveniles which had recently left the brood pouch were also widespread, and it is apparent that breeding goes on during most if not all of the year.

Another possible explanation for the seasonal change in catch is that the population inhabited deeper water in March and November than in July. Some evidence for this is found in a comparison of day and night hauls. In both March and November the mean number per positive haul was much greater for the night hauls than for the day hauls, nearly five times as great in March and more than three times as great in November. These differences suggest that diurnal vertical movements were occurring during these months, and that during the day part of the population was below the level of the net hauls. In July, however, there was almost no difference between the mean number per station for the day hauls and that for the night hauls. Here diurnal vertical migrations were very limited or lacking, and probably at least most of the populations were living at depths not greater than 70 meters.

2. Northwestern Pacific: I have been able to examine a limited number of plankton samples from the northwestern Pacific. In addition to *Albatross* samples, principally from the Sea of Japan, I have studied specimens from *Carnegie* stations, material sent to me by Motoda, Nakai, and Yang, and a few specimens from salmon stomachs forwarded to me by William Aaron of the University of Washington.

All the samples from the Japan and Okhotsk Seas contained *P. japonica.* In addition *P. japonica* was found at *Albatross* stations 4805 (east of Iturup Island, Kuriles) and 4806 (east of Cape Yerimo, Hokkaido), and in one of Motoda's samples from east of Cape Esan, Hokkaido. In these latter three samples *P. pacifica* also occurred, but in much smaller numbers than *P. japonica.*

Further east only *P. pacifica* occurs. Detailed planktonic surveys are needed to establish the eastern boundary of *P. japonica. P. pacifica* extends to Japanese coastal waters, but does not occur in the Japan Sea and probably not in the Sea of Okhotsk, where it is replaced by the larger *P. japonica.*

In 1948 Irie reported on the distribution of a number of pelagic amphipods in waters adjacent to Japan, including a species of *Parathemisto* which was listed as "*Parathemisto* sp. A." In a later paper (1957b) this species is illustrated under the name *Themisto gracilipes* Norman, but the illustrations are clearly of *Parathemisto japonica.* Probably both *P. japonica* and *P. pacifica* were present in Irie's collections, and possibly *P. gracilipes* in the stations south of Japan.

In figure 8 I have plotted the distribution of *Parathemisto* in the vicinity of Japan from Irie's data. To these data I have added some *Albatross* and *Carnegie* stations as well as the localities reported by Nakai (1955). While the occurrences in the Japan and Okhotsk Seas are undoubtedly *P. japonica*, those east of Japan probably include both *P. japonica* and *P. pacifica*. Since the temperatures limiting southward penetration are similar for *P. japonica* in the Japan Sea (see p. 366) and for *P. pacifica* along the California coast, Irie's data on the occurrence of *Parathemisto* east of Japan can be applied to both *P. japonica* and *P. pacifica*. His data show that these species are most abundant north of Japan. Irie (1948) states that *Parathemisto* is abundant between 40° and 50° N., common between 35° and 40° N., but very rare between 25° and 35° N. Figure 8 indicates that the southern boundary falls at about 36° N.

P. pacifica inhabits cold water, and the extent of its southern penetration along the eastern coast of Japan must depend on the relative influences of the Kuroshio and the Oyashio. The warm Kuroshio leaves the coast of Japan and turns east or northeast at Cape Inubozaki (35°40′ N.), with a variable amount of north-south meandering (Masuzawa, 1955). Koizumi (1953) reported on the temperature variations at 39° N., 153° E., a locality which is sometimes covered with water of Kuroshio origin, at other times with cold water of Oyashio origin. Here the temperature at a depth of 25 m. in 1948 varied from 10.80° C. in March to 21.64° C. in September. Clearly the southern boundary of the Oyashio and of its inhabitants, including *P. japonica* and *P. pacifica*, is subject to fluctuation.

In the region where the two current systems meet, the Oyashio may underlie the Kuroshio to a limited extent. Tanaka (1953) observed that in the waters near the Izu Peninsula the warm-water copepod species of the Kuroshio were confined to the upper 200 m., while the cold-water species of the Oyashio were obtained chiefly from below 200 m.

Recently several Russian biologists of plankton have set up faunal zones and zoogeographic boundaries in the region east of Japan and southeast of the Kurile Islands. This work is summarized by Beklemishev and Semina (1956) and by Bogorov (1958). *P. japonica* (=*P. japonica* + *P. pacifica*) is listed by Bogorov and Vinogradov (1955) as an inhabitant of their boreal epipelagic zone, extending south to about 40–42° N. and having surface temperatures of from 9–15° C. This zone is also characterized by the copepods *Calanus tonsus* and the chaetognaths *Sagitta elegans* and *Eukrohnia hamata*. Brodsky (1955a) refers to it as the "*Calanus tonsus* Zone," and it undoubtedly corresponds to Hida's (1957) "Subarctic Zone" in the mid-Pacific.

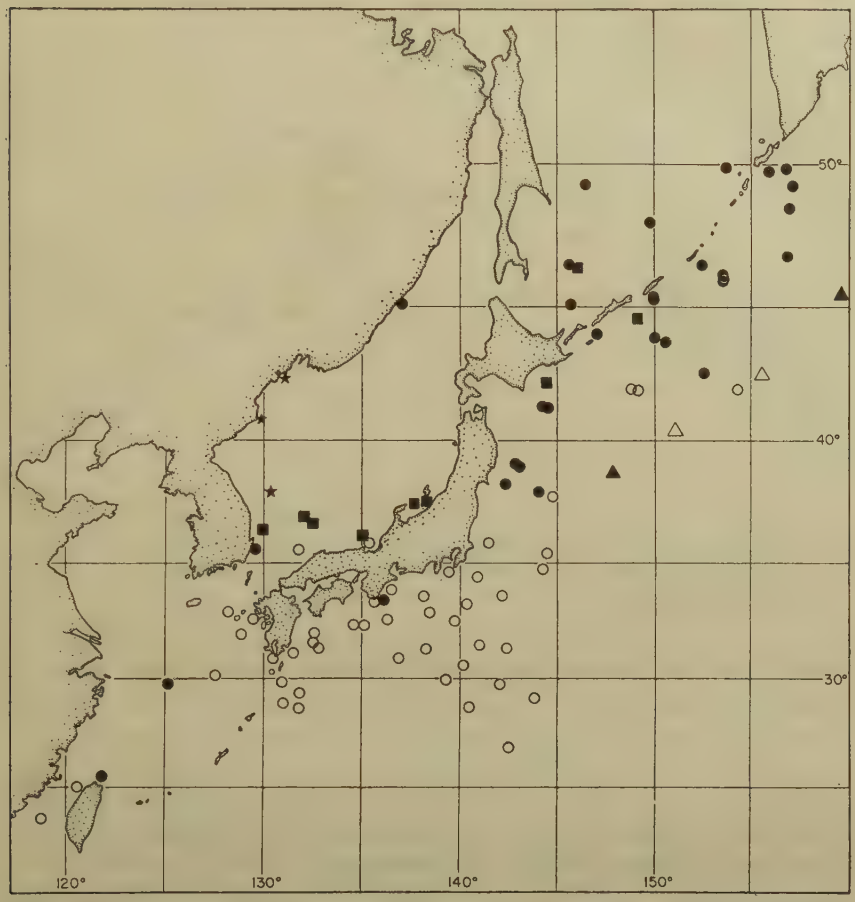

FIGURE 8.—Distribution of *Parathemisto pacifica* and *P. japonica* in the northwestern Pacific. Positive stations indicated by solid symbols, negative stations by open symbols. Circles, stations reported by Irie (1948). Squares, *Albatross* stations. Stars, stations reported by Nakai (1955). Triangles, *Carnegie* Stations. The two southernmost stations reported by Irie probably had *P. gracilipes*. Only *P. japonica* was present at the *Albatross* stations in the Japan and Okhotsk Seas; both *P. japonica* and *P. pacifica* at the two *Albatross* stations east of Japan; only *P. pacifica* at the *Carnegie* stations.

3. North Pacific Ocean: In figure 9 I have attempted to show the probable limits of distribution of *P. pacifica* across the entire North Pacific. The approximate southern boundary east of about 160° W. is based not only on CCOFI material, but also on samples from cruise VII of the *Carnegie* and the *Northern Holiday* Expedition of the Scripps Institution of Oceanography. In the region between 170° E. and 160° W., no collections have been made available to me, but extensions of the boundaries in the CCOFI area and in the northwestern

than the March or November generations. If this explanation is correct, it means that several generations are produced each year, with each generation living only a few months or less. In contrast, Dunbar (1957) proposes a life cycle of 18 months to 2 years for *P. libellula* in the eastern Canadian Arctic, and Bogorov (1940) gives evidence for a 2-year life cycle for *P. abyssorum* in the Barents Sea.

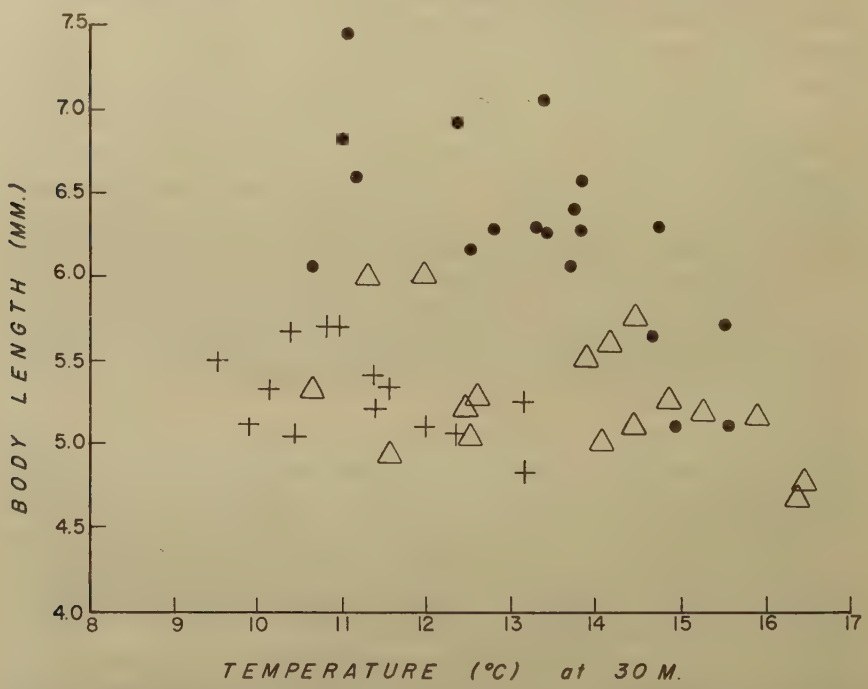

FIGURE 10.—*Parathemisto pacifica* Stebbing, relation between body length and temperature at a depth of 30 meters. Plus signs, cruise 1, March 1949; circles, cruise 5, July, 1949; triangles, cruise 9, November 1949. Each symbol represents the average length of the adult females from one station.

However, there is considerable evidence, much of it summarized by Dunbar, that marine poikilotherms from warm water grow to maturity more rapidly than do those from cold water. It is reasonable to suppose that *P. pacifica* passes through its life cycle more quickly than its Arctic relatives.

2. The *Parathemisto* population sampled in July may be older, hence larger individuals of the generation sampled in March. The November population, composed of smaller individuals than the July population, must represent a different generation. This interpretation requires that an individual breed more than once during its lifetime. Dunbar concluded that *P. libellula* breeds only once and then dies, but

this finding is not necessarily true for *P. pacifica*. On the contrary, examination of the ovaries of females with eggs or young in the brood pouch provides strong evidence that more than one generation of offspring is produced by the individual female. The ovaries can be readily seen through the transparent ventral body wall of the pereon; they lie on either side of the posterior midgut and anterior hindgut, above and in close association with the digestive diverticulae. In the ovigerous females that I examined, I saw new groups of eggs developing in the ovaries. The presence of a second group of eggs indicated that another clutch of eggs would be laid.

The above evidence indicates that the individual *P. pacifica*, in contrast to *P. libellula*, produces at least two and perhaps more sets of offspring during its lifetime. It is therefore possible that the July-breeding females are the older and larger members of the generation sampled in March, and that they have already produced one or more litters.

3. Because of a seasonal difference in vertical distribution, larger specimens, which lived in deeper water in March, were within the range of the nets in July. Earlier in this paper it was deduced from a comparison of day and night hauls that the *Parathemisto* population lives nearer the surface in July than in March or September. This habit would account for the larger average length as well as the larger numbers of the specimens collected in July. It is well established that in most, but not all zooplankters, the adults live at greater depths than the juveniles, and adults from deeper water average larger than those nearer the surface. Bogorov (1940) found that the young of *P. abyssorum* in the Barents Sea prefer the upper water layers, but according to Dunbar (1946), *P. libellula* has a marked phototropism and stays near the surface, especially on sunny days. In the Gulf of Maine the young *P. gaudichaudii* are most numerous near the surface, while adults occur mainly in net hauls made below the surface (Bigelow, 1926, p. 163).

4. The larger individuals collected in July lived in colder waters to the north in March and were carried south by the California Current. This hypothesis would not account for the smaller size of the November specimens, which would have to belong to a different generation. The California Current is slow and meandering, and has numerous eddies. It seems unlikely that any considerable segment of the *Parathemisto* population that inhabits the California Current is unable to maintain itself latitudinally against the southward flow. I regard this explanation as highly improbable.

It is improbable that any of the above explanations can, by itself, fully account for the observed seasonal variation in size of *P. pacifica*. The cruises from which I have studied material are too widely sepa-

rated in time to provide the details needed for a satisfactory explanation.

Development: As in almost all amphipods, the eggs and early juveniles are carried loosely in the marsupium between the ventral wall of the pereon and the oostegites. Counts made of the number of eggs ranged from 20 to 60, with an average number of about 35. Behning (1939) found up to 200 eggs per female in the much larger (8.5–17 mm.) *P. japonica.*

When the young leave the marsupium there is almost no difference between the sexes. The young are miniature editions of the adults, except that there are fewer setae on the pereopods, and the flagella of antennae 1 and 2 are unisegmental in both sexes. Of course the oostegites are entirely absent from the female.

Even at this early stage it is possible to distinguish males from females in almost all cases by the shapes of the antennal flagellae, especially those of antennae 1. In the early juvenile male the flagellum of antenna 1 is longer and broader; the portion distal to the sensory filaments, which in the female is shorter and sharply pointed, tapers more gradually and is half the length of the whole flagellum. The flagellum of antenna 2 is also longer and heavier in the male.

As development proceeds, the male flagellum becomes segmented. In males about to molt, the segmentation which the flagellum will have during the following instar can be seen through the cuticle. Consequently it has been possible to estimate the number of instars from the last stage characterized by a unisegmental flagellum to the adult male stage.

The instars may be defined as follows:

1. Flagellum of antenna 1 short, unisegmental.
2. Flagellum slightly shorter than height of head, 8–10 segmented.
3. Flagellum about as long as pereonites 1–5 combined, 11–12 segmented.
4. Adult male, flagellum about as long as pereon, 13–15 segmented.

The additional segments are added from the distal end of the long first flagellar segment. In the male about to molt, it can be seen that two or three segments are formed here. The segments distal to the first one apparently do not divide further after being formed.

This method of forming additional segments differs from that of the gammarids *Pontoporeia affinis* Lindström (Segerstråle, 1937) and *Gammarus chevreuxi* Sexton (Sexton, 1924). In *Pontoporeia* males, new segments are formed, as in *Parathemisto*, by division of the proximal segment. At first this is the only method, but later the remaining segments begin to divide into two, after which they do not divide again. In the female the distal segments do not divide, and the process is essentially similar to that in *Parathemisto.* In

Gammarus new segments are formed by division of the two (or three in older animals) proximal flagellar segments with the result that two (or three) new segments are added at each molt. Segerstråle found that the antennal segments of the male *Pontoporeia* become greatly lengthened at the last molt; lengthening at this time must also occur in *Parathemisto* (compare figs. 2*a* and 3*a*).

It is apparent that after an unknown number of instars during which the antennal flagellum remains unisegmental, the male *Parathemisto* passes through a minimum of three additional instars. According to Mogk (1926), the male *Phronima sedentaria* (Forskål) passes through five instars with an unsegmented flagellum. Segments first appear in the sixth instar, and the male reaches maturity in the seventh instar. In *Phronima atlantica* Guérin segmentation is also first apparent in the sixth instar, but the adult condition is not reached until the eighth instar.

In the first stage after leaving the marsupium, the flagellum of antenna 1 of *Gammarus chevreuxi* Sexton (Sexton, 1924), *G. fasciatus* Say (Clemens, 1950), and *Pontoporeia affinis* Lindström (Segerstråle, 1937) consists of four segments. By the fourth stage the segments number 8 for *G. chevreuxi* and 9 for *G. fasciatus;* and in the fifth postmarsupial instar there are 10 and 9 segments, respectively. On the assumption that the first instar of *P. pacifica* with segmented flagella corresponds to the fourth or fifth instar of *Gammarus*, we can postulate that there are 3 or 4 postmarsupial instars of *Parathemisto* with unsegmented flagellae, or a total of 5 to 6 postmarsupial molts required to attain sexual maturity. In gammarideans which have been studied, from 7–14 molts are required (Sexton, 1924, 1928; Roux, 1933; Clemens, 1950; Kinne, 1953, 1959).

Oostegites first appear in the female when she is quite small (3.1 mm. in the earliest stage illustrated). At this stage, the oostegites are very small lobes arising mediad to the gills and only about one-third the length of the gills. During subsequent molts the oostegites increase in size, and in the adult they are transparent, membranous and much larger than the gills. No marginal setae are present. Development of the oostegites in *P. libellula* is identical (Dunbar, 1957).

The size at which maturity is reached varies widely. As an example, 382 females and 491 males from station 702, cruise 1, were examined for maturity, judged in the males by the elongate antennae and in the females by the presence of fully developed oostegites. The results are given in table 1.

The males attain maturity at a slightly smaller size than the females, though not necessarily at a younger age.

Food: Reports of the food habits of *P. gaudichaudii* and *P. libellula* have been given by Bigelow (1926, p. 107) and Dunbar (1946) respec-

TABLE 1.—*Length and maturity in* Parathemisto pacifica.

Specimens	*Length (mm.)*											
	3.6	*3.8*	*4.0*	*4.2*	*4.4*	*4.6*	*4.8*	*5.0*	*5.2*	*5.4*	*5.6*	*5.8*
Females:												
Number examined	–	165	32	37	24	23	29	24	20	17	11	7
Percent mature	–	0	3	0	13	35	48	83	90	77	82	100
Males:												
Number examined	165	55	60	63	51	26	26	20	6	7	–	–
Percent mature	0	2	0	21	41	74	90	100	83	100	–	–

tively. Both species are predominately carnivorous, sometimes cannibalistic, but also ingest some vegetable matter.

I have examined the midgut contents of a few specimens of *P. pacifica.* Consisting of minute greenish or brownish particles, much of the material was unrecognizable, but some fragments of diatoms and crustaceans were identified. The crustacean parts included copepod swimming legs and mouthparts (one mandible was recognizable), spines of undetermined origin, and crystalline cones from compound eyes. It seems reasonable to conclude that the food habits of *P. pacifica* are similar to those of *P. gaudichaudii* and *P. libellula.*

ANATOMY OF DIGESTIVE TRACT: The structure of the alimentary canal of *P. libellula* is considered briefly by Dunbar (1946). He describes an interesting "gastric apparatus" formed of dorsolateral and ventral sheets projecting backward in the midgut, which he compares with the peritrophic membrane of insects and onychophorans. Dunbar also states that there are no caeca or diverticula of any kind. On this point my findings do not agree with his.

In *P. pacifica* a pair of caecae arise laterally from the midgut near its anterior end. They extend posteriorly along the entire length of the pereon and run along in close association with the lateral parts of the midgut and with the gonads which lie dorsal to them. The caecae usually have a coarsely vesicular appearance; in section the vesicles are seen to be large vacuolate cells. The vacuoles are filled with an oily or fatty material, and vary greatly in size. In some individuals the vacuolate cells are so large that the lumena of the caecae are nearly obliterated; in others the vacuoles are small and the lumena well defined.

Contrary to Dunbar's statement, a pair of caecae is also present in *P. libellula.* Because they are closely applied to and partially fused with the gut wall, their true nature is not obvious in dissected specimens, and if the lumen is sufficiently encroached on by the large

vacuolate cells, it may be difficult to interpret the caecae correctly in sectioned material. I have also found the same caecae in *P. gaudichaudii* from the Gulf of Maine, and they are probably characteristic of all species of *Parathemisto*.

Although I have not made a detailed study of the histology of the digestive caecae, it seems reasonable to suppose that their principal function is the storage of reserve food supplies. The large fat cells can scarcely be interpreted otherwise. In some specimens of *P. gaudichaudii* which had been stored in alcohol for a long period, the caecae have the appearance of a foamy network, and must be made up almost completely of fat cells. I have found no structure in *Parathemisto* comparable to the fat body of gammarids, and the storage of reserve food in this genus is probably carried out by the digestive diverticula. It is interesting to note that Nakai (1955) found the crude fat content of *P. japonica* from Korean waters to be nearly 40 percent of the dry weight.

Parathemisto (Parathemisto) japonica Bovallius

FIGURES 2,*b–i;* 3,*f–l;* 8; 16,*c*

Parathemisto japonica Bovallius, 1887, p. 21; 1889, pp. 258–263, pl. 12, figs. 17–43.—Behning, 1939, pp. 362–363, fig. 1.
Parathemisto sp. (11) Yamada, 1933, p. 7, pl. 2, fig. 10,*a–g*.
Parathemisto sp. Nakai, 1955, pp. 14–15.
Parathemisto sp. A. Irie, 1948, p. 36.
Themisto gracilipes Norman, Irie, 1957b, p. 353, figs. 16–1, 16–2.
Themisto japonica, Irie, 1959, pp. 20, ff.

DIAGNOSIS: Total length of adult ♀, excluding antennae, 9–17 mm. Identical with *P. pacifica* in almost all characters except size, but female antenna 2 much longer than antenna 1, slightly longer than head plus first 3 pereonites. Setae of pereopods more conspicuous, more numerous on gnathopods.

REMARKS: While I am not unalterably convinced that *P. japonica* and *P. pacifica* are distinct species, all the evidence at my disposal leads to this conclusion. Except for mutilated specimens, I have had almost no difficulty in assigning specimens to one or the other species. The geographic ranges are different, with some overlap east of northern Japan and the southern Kuriles. In the three samples where both species occurred, I have found no intergrades, and thus no evidence of interbreeding.

Since the number of pereopodal setae increases with age in some species of hyperiids (unpublished observation), it may be argued that *P. japonica* is an older and larger form of *P. pacifica*. However, it is possible to distinguish the young stages of the two species. Antenna 2 is longer than antenna 1 even in very young specimens of *P. japonica*. The difference in the development of setae on pereopod 6,

especially on the posterior margin of the propodus, is shown in figure 2*j* of a 7.0 mm. adult female *P. pacifica* and figure 2*e* of a 6.7 mm. juvenile *P. japonicus*, both of which were taken in the same net tow off Cape Esan, Hokkaido, Japan.

The correlation between temperature and body length in *P. pacifica* raises the possibility that the large size of *P. japonica* is attributable to the low temperatures at which it lives. *P. pacifica* is abundant in the Gulf of Alaska, where adult females commonly measure 6.0–7.0 mm. in length. This size is much smaller than the size of *P. japonica*, and yet surface temperatures in the Gulf of Alaska are similar to those in the colder parts of the Sea of Japan (compare Robinson, 1957, fig. 18, and Uda, 1934, figs. 5 and 9).

With this evidence, the best course is to treat *P. japonica* and *P. pacifica* as closely related, but distinct, species. If intensive collections from the region of overlapping distributions should reveal extensive intergradation, it would then be necessary to reduce their status to that of subspecies. In the limited number of samples at my disposal, however, there is no indication of such intergradation.

The Japanese zoologist Zinziro Nakai believes that the hyperiid which I have described as *P. japonica* Bovallius is an undescribed species of *Parathemisto*. He has assigned to it the Japanese name "Usumurasaki-uminomi" (light purple sea flea) and intends to describe it as a new species (Nakai, 1955). Nakai states (in litt., Oct. 23, 1954) that his decision is based on many discrepancies between Bovallius' descriptions and the structure of specimens from Japanese waters, and on Bovallius' statement (1889) that *P. japonica* occurs in the subtropical region as well as in the northern temperate region of the Pacific. Nakai believes that *P. japonica* is distributed south of Japan and has not been discovered since Bovallius' description of 1889, while "usumurasaki-uminomi" is the common species found north of Japan.

In my opinion, Nakai places too much confidence in the detailed accuracy of Bovallius' descriptions and illustrations. I believe the differences that Nakai finds between Bovallius' account of *P. japonica* and "usumurasaki-uminomi" can be explained as inaccuracies of Bovallius or as variations in the structure of *P. japonica*.

Distribution: Okhotsk Sea, Sea of Japan, western north Pacific off the east coasts of northern Japan and the southern Kuriles.

East of Japan and the southern Kuriles, *P. japonica*, like *P. pacifica*, inhabits Subarctic Water and penetrates about as far south along the Japanese coast as the cold Oyashio. The extent of its eastward distribution is unknown, but at some distance it is replaced by *P. pacifica*.

In the Sea of Japan the scattered records from *Albatross* stations show that *P. japonica* extends south nearly to the Straits of Korea.

The findings of Yamada (1933) are more instructive. In his report on plankton collected from a series of stations off both coasts of Korea, he found *P. japonica* present off the east coast south to nearly 38°, but absent from the Tusima Straits and the Yellow Sea. This distribution correlates well with the hydrography of the Sea of Japan. As Uda (1934) has shown, the water on the Asiatic mainland side is much colder than that on the Japanese side. The cold water flows south along the mainland coast (Liman Current) to the latitude of about 36°–38° N. and forms several counterclockwise eddies as it flows. Only a small amount of mixing occurs between this cold water, presumably formed by excessive cooling in winter, and the warm, north-flowing water of the Tusima Current, a branch of the Kuroshio.

Yamada's findings suggest that *P. japonica* is distributed in the Sea of Japan according to the extent of the cold water, as Tokioka (1940) found for the chaetognath, *Sagitta elegans*. The occurrence of *P. japonica* at *Albatross* stations along the west coast of Honshu makes this hypothesis improbable. Uda's (1934) isotherm charts show that in June most of the Sea of Japan is characterized by temperatures at least as low as those of the southern boundary of the Oyashio. The Oyashio boundary temperatures in Uda's charts are 17°–19° C. at the surface and at 25 m., about 17° at 50 m., and about 15° at 100 m. Most of the water of the Sea of Japan at these depths is as cold or colder, while the water of the southward-flowing current in the west is considerably colder. Hence a wide distribution of *P. japonica* in the Sea of Japan is to be expected from our knowledge of its distribution off the east coast of Japan.

It is reasonable to believe that *P. japonica* evolved from *P. pacifica* or from a common ancestor of both species as a result of geographical isolation. The current patterns in the Japan Sea provide little opportunity for *P. pacifica* to enter from the Pacific Ocean. Almost all the water entering the Sea of Japan is warm water derived from the Kuroshio; only a very small quantity of cold water enters through Tartary Strait between the Asiatic coast and Sakhalin Island. Water leaves the Japan Sea by way of the Straits of Soya (La Pérouse) and Tsugaru, north and south of Hokkaido, respectively. Information concerning water movements in the Okhotsk Sea is still scanty. According to Bruns (1958) there is some exchange of water with the Pacific Ocean through the Kuriles. The very limited collections available to me indicate that this exchange of water has been insufficient to allow *P. pacifica* to become established in the Okhotsk Sea.

Actually, therefore, the *P. japonica* population in the Okhotsk Sea and especially in the Sea of Japan is effectively isolated from extensive gene flow from the *P. pacifica* population. The three northwestern Pacific occurrences of *P. japonica* reported in this paper may be ex-

plained as being derived from the Japan or Okhotsk Seas. For some as yet unknown reason, *P. japonica* has not been able to extend its range far beyond the immediate vicinity of its site of origin.

Parathemisto (Parathemisto) abyssorum Boeck

FIGURE 11,*j–k*; 12–13

Parathemisto abyssorum Boeck, 1870, p. 87(7).—Barnard, 1959, pp. 125–127, pls. 17–19.

Themisto abyssorum (Boeck), Stephensen, 1923, pp. 20–24, chart 4; 1924, pp. 95–97, figs. 36–38; 1944, p. 12.—Shoemaker, 1930, pp. 132–133; 1955, p. 72.

DIAGNOSIS: Length of adult 10–21 mm. Larger and more slender than *P. pacifica*, and head more roundly produced. Maxilliped without a distal row of setae on the basal plate. P1–4 with more surface setae than in *P. pacifica*; posterior margin of propodus of P1 serrate and bearing several long setae. Carpal process of P2 with long end spine. In length P5>P7>P6; no long spines at posterior distal corners of carpi; dactyls not pectinate. Peduncle of uropod 3 about 3 times as long as telson.

DISTRIBUTION: Ekman (1953, p. 340) mentions *P. abyssorum* as an example of an "arctic-bathy-subarctic" species. In this category he includes plankters which live primarily in Arctic waters, but are also found in deep water in lower latitudes. A detailed discussion of the distribution of *P. abyssorum* in the Atlantic is given by Stephensen (1923, pp. 22–24, chart 4). Found throughout the Arctic and Sub-Arctic Atlantic, it is very common in the vicinity of Greenland and between Norway and Iceland. Stephensen believes that Bonnier's (1896) record of 9 mm. ovigerous *P. oblivia* taken at a depth of 950 m. in the Bay of Biscay should be referred to this species. On the western side of the Atlantic it occurs occasionally in the Gulf of Maine (Bigelow, 1926) and is widely distributed in and around the Gulf of St. Lawrence (Shoemaker, 1930; Bousfield, 1951). Bousfield believes that the permanent deep layer of very cold water in the Gulf of St. Lawrence enables the species to breed there successfully, as evidenced by the large numbers of young and immature stages taken near the surface.

I have not found *P. abyssorum* in any plankton collections from the Pacific Ocean. It was, however, the most commonly collected amphipod during the 1950 and 1951 expeditions of the *Burton Island* to the Beaufort Sea and in the 1953 expedition to Amundsen Gulf and Prince of Wales Strait. Station positions and locality records for *P. abyssorum* are shown in figure 12. Plankton hauls were made vertically with a one-half-meter Nansen type plankton net. In 1950 the hauls were made from various depths, usually 100–0 m., and in 1951 all

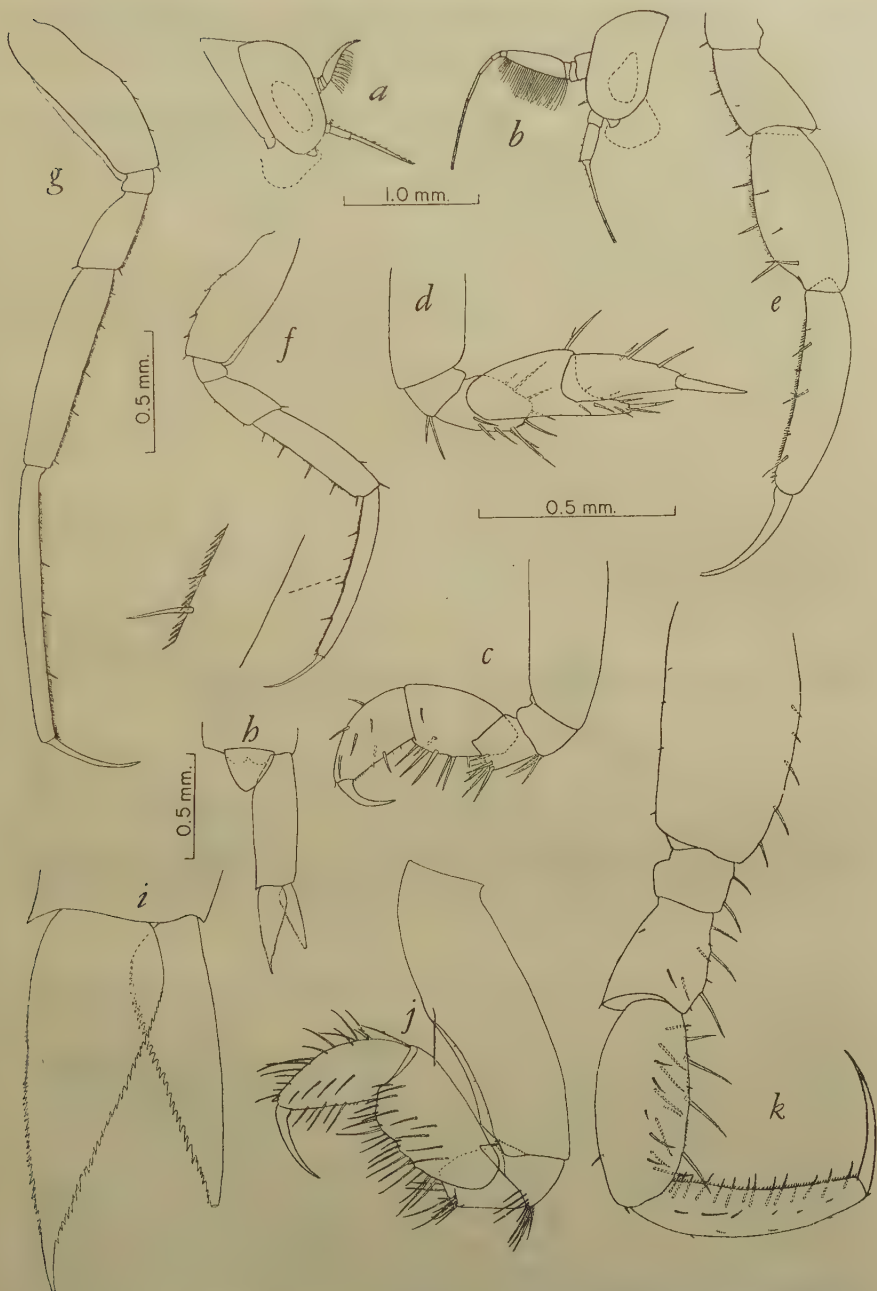

FIGURE 11.—*Parathemisto gracilipes* (Norman), Eastern Sea, west of Kyusyu, Japan: *a*, Head, female; *b*, head, male; *c*, pereopod 1, male; *d*, pereopod 2, male; *e*, pereopod 3, male; *f*, pereopod 5, female; *g*, pereopod 5, male; *h*, uropod 3 and telson, female; *i*, distal end of uropod 3, female. *Parathemisto abyssorum* Boeck, juvenile female, Beaufort Sea, west of Banks Island, U.S.S. *Burton Island* 1950 cruise, station 44: *j*, Pereopod 1; *k*, pereopod 3. Scale same for *a–b*, *c–e*, and *f–g*.

hauls were 100–0 m. except where the depth of the water was less than 100 m. In 1953 hauls were made from the bottom (usually less than 100 m.) to the surface.

In both 1950 and 1951 *P. abyssorum* occurred at about half the stations occupied and in about the same numbers. The average number per station (adjusted to 100 m. vertical tow) was 2.3 in 1950 and 2.6 in 1951. Distribution in the Beaufort Sea appeared not to be associated with variations in temperature or salinity.

P. abyssorum was somewhat less numerous in the 1953 *Burton Island* samples, and was captured at only 4 of the 25 stations in the Prince of

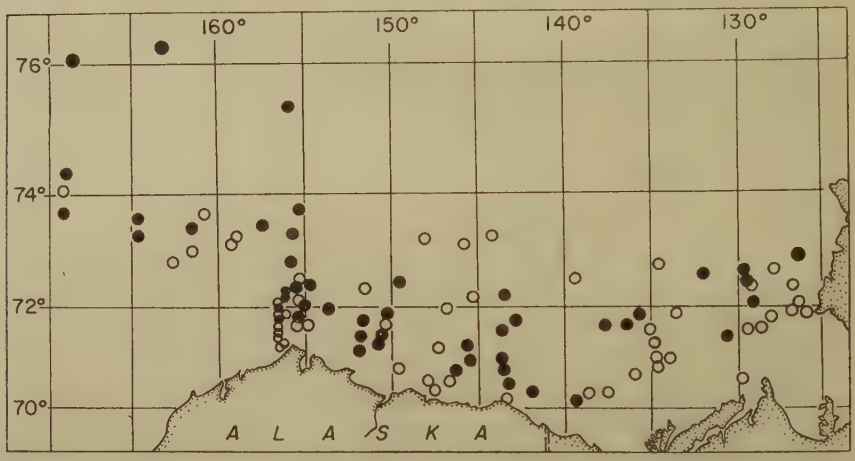

FIGURE 12.—*Parathemisto abyssorum* Boeck, distribution in the Chukchi and Beaufort Seas, U.S.S. *Burton Island* 1950 and 1951 cruises combined. Solid circles, positive stations; open circles, negative stations.

Wales Strait. The average number per station was 0.75; the average number per positive station, 1.50.

All the specimens of *P. abyssorum* collected on the *Burton Island* cruises were juvenile, with the exception of one ovigerous female, 14 mm. in length, taken at station 3, off Cape Parry, in a tow from 420 m. to the surface, August 8, 1953.

Little is known about the life history of *P. abyssorum*. Bogorov (1940) studied the life cycle in the Barents Sea and concluded that spawning occurs in "the second half of the winter season (about February)." He further concluded that the individual requires 2 years to grow to maturity, breeds once, and dies. The breeding season appears to be more prolonged than indicated by Bogorov, since at least some breeding occurs in the Beaufort Sea in August (see above), and Stephensen (1933) reported ovigerous females taken June 12 and

July 14 in waters west of Greenland. In the collections of the U.S. National Museum is a lot consisting of three adult males, 13, 14, and 14.5 mm. in length, and a female 14.8 mm., with fully developed oostegites, taken on May 18, 1902, between the Shetland and Faroe Islands.

Several records of *P. abyssorum* or *P. oblivia* in the Pacific Ocean are probably erroneous, since the authors almost certainly had *P. pacifica* or *P. japonica*. These include the records of Shoemaker (1930) and Thorsteinson (1941) from near Nanaimo, British Columbia, and that of Holmes (1904) from Humboldt Bay, Popof Island, Alaska (about 55° N., 161° W.). Possibly the specimens of "*P. oblivia*" from stations 13 and 14 of the Canadian Arctic Expedition (Shoemaker, 1920) were *P. japonica*, and those from stations 21 and 27 were *P. abyssorum*. Irie's (1957a) record from the Tusima Straits is probably *P. japonica*.

The puzzling thing about the distribution of *P. abyssorum* is that it has not been able to establish itself in the Pacific (fig. 13). This absence cannot be simply a matter of temperature, since the Okhotsk Sea and the western Bering Sea are regions of very low temperatures. In fact *P. libellula*, an Arctic species which does not penetrate as far to the south in the Atlantic as *P. abyssorum*, occurs in the Bering and Okhotsk Seas.

Three possible explanations may be given for the absence of *P. abyssorum* from the Pacific:

1. The current flow through the Bering Strait has made it mechanically impossible for *P. abyssorum* to enter the Pacific Ocean. The hydrographic evidence for a northward flow of water from the Bering Sea into the Chukchi Sea (Barnes and Thompson, 1938; LaFond and Pritchard, 1952) is corroborated by Johnson's (1956) report of the presence of characteristic Bering Sea copepods in the Chukchi Sea (*Eucalanus bungii bungii* Johnson, *Metridia lucens* Boeck). While the penetration of Arctic plankters into the Pacific would be retarded by this northward current, it is unreasonable to suppose that it would be completely inhibited. On the extreme west of Bering Strait there appears to be some movement of water southward, and Sewell (1948, pp. 399–401) believes that this movement has carried certain Arctic planktonic copepods into the north Pacific.

2. *P. abyssorum* is unable to compete successfully with the closely related north Pacific species, *P. japonica* and *P. pacifica*. All three species are very similar in structure and probably occupy similar if not identical ecologic niches. Possibly the Pacific species evolved during a time of isolation of the Pacific from the Arctic by emergence of Bering Strait. Bering Strait has been above sea level during much of geologic history. Hopkins (1959) has recently reviewed the Cenozoic history of the Bering Land Bridge. Evidence of the

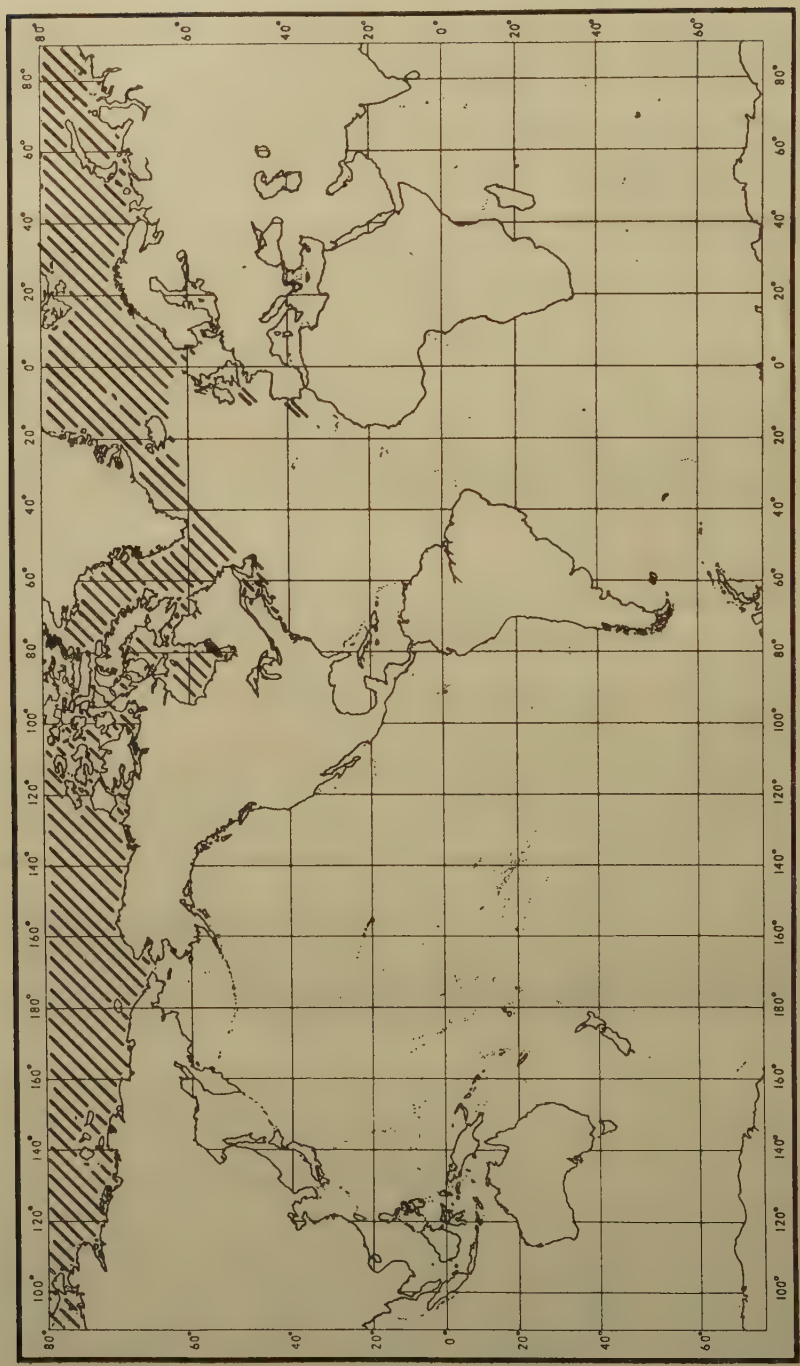

FIGURE 13.—*Parahemisto abyssorum* Boeck, world distribution. The records south of Ireland and west of Portugal are from deep water.

interchange of land mammals strongly suggests that the bridge was submerged during middle Eocene time (Simpson, 1947a, 1947b), although physical evidence in support of this submergence has not yet been found in Alaska or the islands of the Bering Sea. During most of the remainder of the Tertiary Period the bridge was above sea level. After middle Pleiocene time but before the beginning of the Pleistocene epoch, the bridge was again submerged. The bridge emerged during each glacial interval and submerged during each interglacial interval of the Pleistocene; it sank below sea level for the last time between 11,000 and 12,000 years ago. There has thus been ample opportunity for the evolution of species in the north Pacific differing from their arctic relatives. If the northward flow of the current in the Bering Strait severely limits the numbers of *P. abyssorum* entering the Bering Sea, it is evident that this species would be markedly handicapped in establishing itself in competition with the abundant *P. pacifica*.

3. *P. abyssorum* avoids shallow water, hence does not enter the shallow Bering Strait. As suggested by the specific name, *P. abyssorum*, according to Stephensen (1923, p. 23), is found, as a rule, where the depth of the sea is considerable, 400–3,127 meters. It occurs in shallower water, as in the Gulf of St. Lawrence, where Bousfield (1951) reports it from stations where the water was less than 100 m. deep, though it was rare in the shallow water inside the Belle Isle Strait. Curiously, Bousfield found that *P. abyssorum* was an indicator of the relatively warm Gulf of St. Lawrence water, rather than, as might be expected of an Arctic species, of the cold water of the Labrador Current, which enters the gulf on the north side of the Belle Isle Strait. It is most abundant at the deep water stations of the gulf, which do not happen to be in the region influenced by the Labrador Current. It probably enters the gulf through Cabot Strait, rather than through the shallow Belle Isle Strait; this entrance also accounts for the larger numbers at the stations in the southern part of the gulf.

The depths of the sea at the stations in the Beaufort and Chukchi Seas occupied by the *U.S.S. Burton Island* ranged from 18 to 4,050 m. The depths at which *P. abyssorum* occurred are summarized in table 2.

The shallowest station at which *P. abyssorum* was taken was 53 m. The entire Bering Strait is less than 50 m. deep, much of it considerably less, and this shallowness may be an important factor in preventing *P. abyssorum* from gaining entrance to the Pacific Ocean. The comparative scarcity of *P. abyssorum* in the Prince of Wales Strait may be related to the shallowness of the water there; the deepest station was 150 m., and only five stations were more than 100 m.

Probably none of the three explanations given above can by itself account for the absence of *P. abyssorum* from the Pacific Ocean. A combination of them may, however, be effective, the shallowness of the Bering Strait and the northward set of the currents preventing all but a small number from entering the Bering Sea, while competition with *P. pacifica* prevents those that do enter from establishing themselves.

TABLE 2.—*Depth of the water and occurrence of* Parathemisto abyssorum *in the Beaufort and Chukchi Seas, 1950 and 1951* Burton Island *Cruises combined.*

Stations	*Depth (meters)*			
	0–100	*101–200*	*201–500*	*500*
Number occupied	23	18	20	44
Number positive	5	7	8	28
Percent positive	21. 7	38. 9	40. 0	63. 6

Subgenus *Euthemisto* Bovallius

Dorsal spines present or absent. Flagellum of female antenna 1 curved, heavier than in subgenus *Parathemisto* (except in *P.* (*E.*) *libellula*). Carpus of P3–4 usually more expanded than in subgenus *Parathemisto*. P5 much longer than P6–7 (except in some females of *P.* (*E.*) *gracilipes*). Peduncle of uropod 3 only slightly produced at inner distal end.

Key to the Species of the Subgenus *Euthemisto*

(Modified from Barnard, 1930)

1. Female antenna 1 slender, straight. Dactyls of P5–7 pectinate at base. **libellula** Lichtenstein
   Female antenna 1 stouter, hooked. Dactyls of P5–7 unarmed at base . . 2
2. Inner ramus of uropod 3 serrate only on outer margin. **gaudichaudii** (Guérin)
   Inner ramus of uropod 3 serrate on both margins 3
3. Inner margin of uropod 3 peduncle smooth throughout. **gracilipes** (Norman)
   Inner margin of uropod 3 peduncle distally serrulate. **australis** (Stebbing)

Hurley (1955) discusses in detail the difficulties in distinguishing between *australis*, *gracilipes*, and *gaudichaudii* in collections from New Zealand waters. The three species show clear differences in general appearances, but these are very difficult to set down in words. Hurley notes that *P. australis* is shorter and stockier than the other species,

with no sign of dorsal spines, and with coarse serrations on the inner ramus of uropod 3. *P. gaudichaudii* is characterized by larger size (up to 18 mm.), very distinct dorsal spination in adults, and the lack of serration along the inner margin of uropod 3 inner ramus and peduncle. In *P. gracilipes* the peduncle of uropod 3 of the very largest specimens appears serrulate when viewed under very high power, but is not at all comparable to that of *P. australis*. The serration of uropod 3 inner ramus is poorly developed in the female of *P. gracilipes*.

Parathemisto (Euthemisto) gracilipes (Norman)

FIGURES 11,*a–i*; 14–15; 16,*b*

Hyperia gracilipes and (?) *H. oblivia* Norman, 1869, p. 287.
Themisto gracilipes (Norman), Stephensen, 1924, pp. 97–103, figs. 39–42 [lit. and syn.]; 1949, p. 54.—Pirlot, 1929, p. 128.—Candeias, 1934, pp. 4–5, fig. 4.
Parathemisto (Euthemisto) gracilipes (Norman), Barnard, 1930, p. 421.—Hurley, 1955, pp. 153–161, figs. 133, 158, 176, 178.
[?] *Parathemisto* sp. (12), Yamada, 1933, p. 8, pl. 2, fig. 12a–e.

DIAGNOSIS: Total length of adult, excluding antennae, 4–7 mm., rarely up to 9 mm. (Stephensen, Mediterranean and Atlantic specimens); 6.5–14 mm. (Hurley, New Zealand specimens); 4.1–5.6 mm. (specimens from Tusima Straits and Eastern Sea). Only slight tendency to dorsal spination. Carpus of P2 extends about two-thirds along propodus, has one stout end spine. Uropod 3, inner ramus pectinate on both margins; inner margin of peduncle finely toothed in male (teeth very inconspicuous or absent in female).

REMARKS: The above diagnosis is based largely on that of Hurley (1955, p. 153), who has studied abundant material of *P. gracilipes*, *P. gaudichaudii*, and *P. australis* from New Zealand waters. I have had at my disposal a limited number of specimens from two surface-plankton tows—one made in Tusima Straits (34°20.7′ N., 130°47.3′ E.) and the other in the East China Sea west of Kyusyu, Japan (32°06.4′ N., 128°57.0′ E.), kindly sent to me by Zinziro Nakai. In addition, Won Tack Yang sent me three lots from off the southern coast of Korea. The characters which Hurley regards as diagnostic for *P. gracilipes* are found in these specimens. The Japanese specimens are small; two adult females measure 4.8 and 5.4 mm., and eight adult males range in length from 4.1–5.6 mm. and average 4.9 mm. The setal armature of the pereopods resembles Stephensen's (1924, figs. 39–41) rather than Hurley's drawings (1955, text-figs. 8–9). This fact may be attributed to the larger size of the New Zealand specimens.

In the Japanese specimens the serrulations of the inner margin of the male and female uropod 3 peduncle are barely discernible under high (×440) magnification, even less evident than that figured by

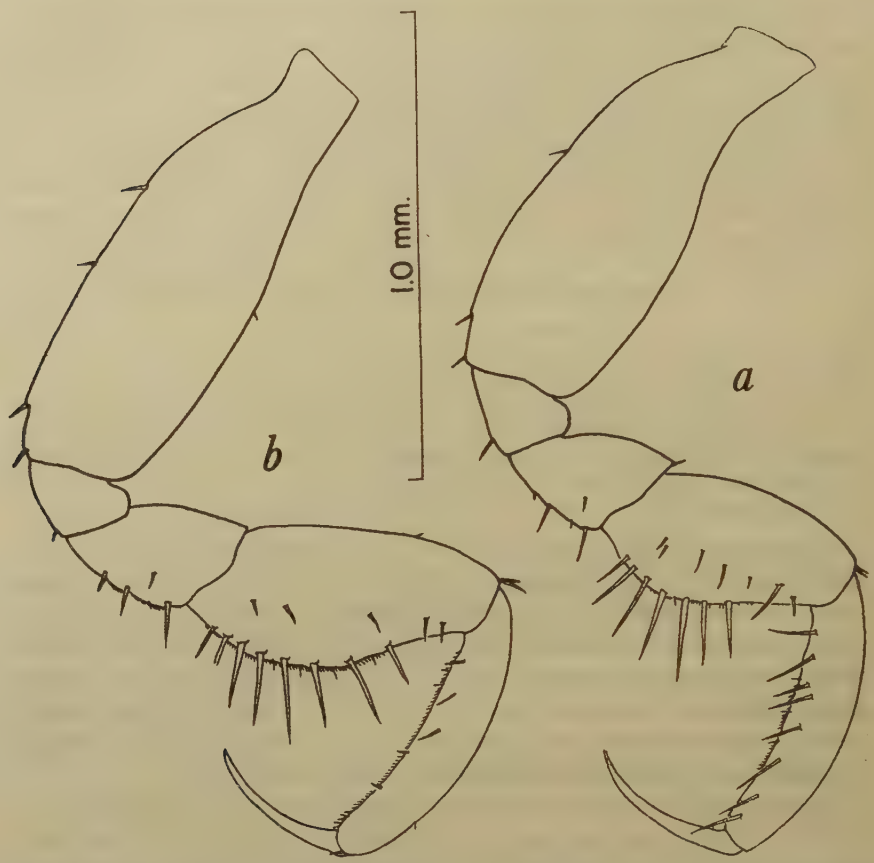

FIGURE 14.—*Parathemisto gracilipes* (Norman), "long-legged" form, adult female from Yellow Sea, west of Mok Po, Korea: *a*, Pereopod 3; *b*, pereopod 4.

Hurley. This near absence of serrulations is also probably due to the small size of the Japanese specimens. As in Hurley's description, the inner margin of uropod 3 inner ramus is more finely serrate in the female than in the male. In the female P5 and P7 are subequal, slightly longer than P6. In the male, P5 is relatively longer; the distal end of P6 propodus reaches about three-fourths to the distal end of P5 propodus.

The Korean specimens agree in general with the Japanese ones, which appear to represent Stephensen's (1924) "short-legged" form, but one lot collected west of Mok Po (34°30′ N., 125°0′ E.), consisting of an adult female and a juvenile, agrees with Stephensen's "long-legged" form, except in the shape of the carpus of P3–4. In the adult female, P6 extends one-fourth the distance down the propodus of P5

and has a high comb of setae on its anterior margin. P3–4 carpus (fig. 6) are of the form typical for *P. gaudichaudii* forma *bispinosa* (=*antarctica*), in which the carpus is wide proximally and narrows distally; the posterior margin is convex in the proximal part and becomes straight or slightly concave distally. A tendency toward this form is evident in the New Zealand specimens illustrated by Hurley (1955, text-fig. 9, Nos. 155–156). According to Stephensen, there are no fine teeth along the posterior margin between the long setae in the female, but these are present in both the New Zealand and Korean specimens.

Yamada (1933) illustrates a "*Parathemisto* sp. (12)" which he found to be widely distributed in the Yellow Sea. Although he did not identify it specifically, he stated that using Barnard's key (1930) the specimens keyed out to *P. gaudichaudii*. This statement implies that the inner margin of the inner ramus of uropod 3 appeared smooth to him. In my Korean "long-legged" *P. gracilipes*, the serrations of this margin are quite weak, and it is possible that they escaped Yamada's notice. If so, his "*Parathemisto* sp. (12)" is *P. gracilipes* rather than *P. gaudichaudii*, for in other respects "*Parathemisto* sp. (12)" agrees reasonably well with my" long-legged" *P. gracilipes*. Yamada's specimens attained a length of 7–8 mm.; this length is short for *P. gaudichaudii*, but about right for *P. gracilipes*. Moreover, on the basis of the temperatures at which they live in other regions, *P. gracilipes*, rather than *P. gaudichaudii*, would be expected to occur in the East China and Yellow Seas.

Although it thus seems probable that Yamada's "*Parathemisto* sp. (12)" is *P. gracilipes*, the possibility remains that his tentative identification of it as *P. gaudichaudii* was correct. This problem cannot be solved until extensive collections from the Yellow Sea are available.

Distribution: Figure 15 shows the known distribution of *P. gracilipes*. It is evident that much remains to be learned about its distribution, especially in the southern hemisphere. The record of Stewart (1913) from off Brazil is probably erroneous, since members of the genus *Parathemisto* are not known to inhabit tropical waters. Stephensen (1949) regarded his identification of specimens from Tristan da Cunha as doubtful.

The collections of the U.S. National Museum contain 7 specimens of *P. gracilipes* collected in the vicinity of the Juan Fernandez Islands by the yacht *Vagabondia*. Comparable in size to Hurley's New Zealand specimens, these specimens range from 7.9–8.5 mm. in length and agree well with Hurley's description.

P. gracilipes lives in warmer water than *P. gaudichaudii*. This preference is clearly shown in the distribution of the two species in the north Atlantic (see figs. 15 and 17; see also Stephensen, 1923 and

FIGURE 15.—*Parahemisto gracilipes* (Norman), world distribution.

1924 and Pirlot, 1939). Bary (1959) showed a similar difference in temperature preference in southern New Zealand waters. The absence of *P. gracilipes* from the Atlantic coast of the United States results from the rapid change of temperature over the range inhabited by *P. gracilipes* so that it literally has no living room. Hurley (1955) pointed out that *P. gracilipes* inhabits more neritic water than *P. gaudichaudii* in the New Zealand area, and Bary's (1959) detailed analysis confirms this view. In the north Pacific the occurrence of *P. gracilipes* in the east China and Yellow Seas may reflect its preference for coastal waters. Both of these seas are shallow and subject to much runoff from rivers.

In the vicinity of Plymouth, England, *P. gracilipes* undergoes a diurnal vertical migration; it moves close to the surface at night and descends during the day (Russell, 1925). Bary's data show evidence of a similar migration in New Zealand waters.

Parathemisto (Euthemisto) gaudichaudii (Guérin)

FIGURES 16,*a*; 17

Themisto gaudichaudii Guérin, 1825, p. 774.
Themisto compressa Goës, Stephensen, 1924, pp. 103–110, figs. 43–49.
Euthemisto compressa (Goës), Chevreux, 1935, pp. 191–192.
Euthemisto bispinosa Boeck, Chevreux, 1935, p. 191.
Themisto gaudichaudii Guérin, Stephensen, 1933, pp. 63–64; 1944, pp. 10–12; 1947, pp. 76–77; 1949, p. 54.—Pirlot, 1939, p. 39.
Parathemisto (Euthemisto) gaudichaudii (Guérin), Barnard, 1930, p. 420; 1932, pp. 280–282 (synonomy).—Hurley, 1955, pp. 161–164, figs. 159–174.
[?] *Parathemisto* sp. (12) Yamada, 1933, p. 8, pl. 2, fig. 12, *a–e*.
Euthemisto antarctica (Dana), Ealey and Chittleborough, 1956, p. 22.

DIAGNOSIS (SLIGHTLY ALTERED FROM HURLEY, 1955): Length of adult, 7–25 mm. Strong dorsal spines in animals of more than 10 mm. total length. Carpus of P2 extends three-fourths along propodus. P3 male carpus widest proximally, width nearly one-half the length; like *P. gracilipes*, but rather more spines on surface and margin; carpus and propodus subequal. P4 male carpus oblong-ovate, width slightly more than one-half the length, fringe of small even bristles on posterior margin; about 12 strong spines. Uropod 2 outer ramus about three-fifths length of inner. Uropod 3 outer ramus two-thirds length of inner; inner ramus with smooth inner margin; inner margin of peduncle entirely smooth. P3 female carpus oblong-ovate and widest proximally, width about two-thirds the length; numerous fine surface spines, 10 marginal spines, marginal bristles throughout. P4 female has about 18 surface spines on carpus.

REMARKS: As Hurley has pointed out, the most dependable criterion by which *P. gaudichaudii* can be identified is the completely smooth inner margins of the peduncle and inner ramus of uropod 3.

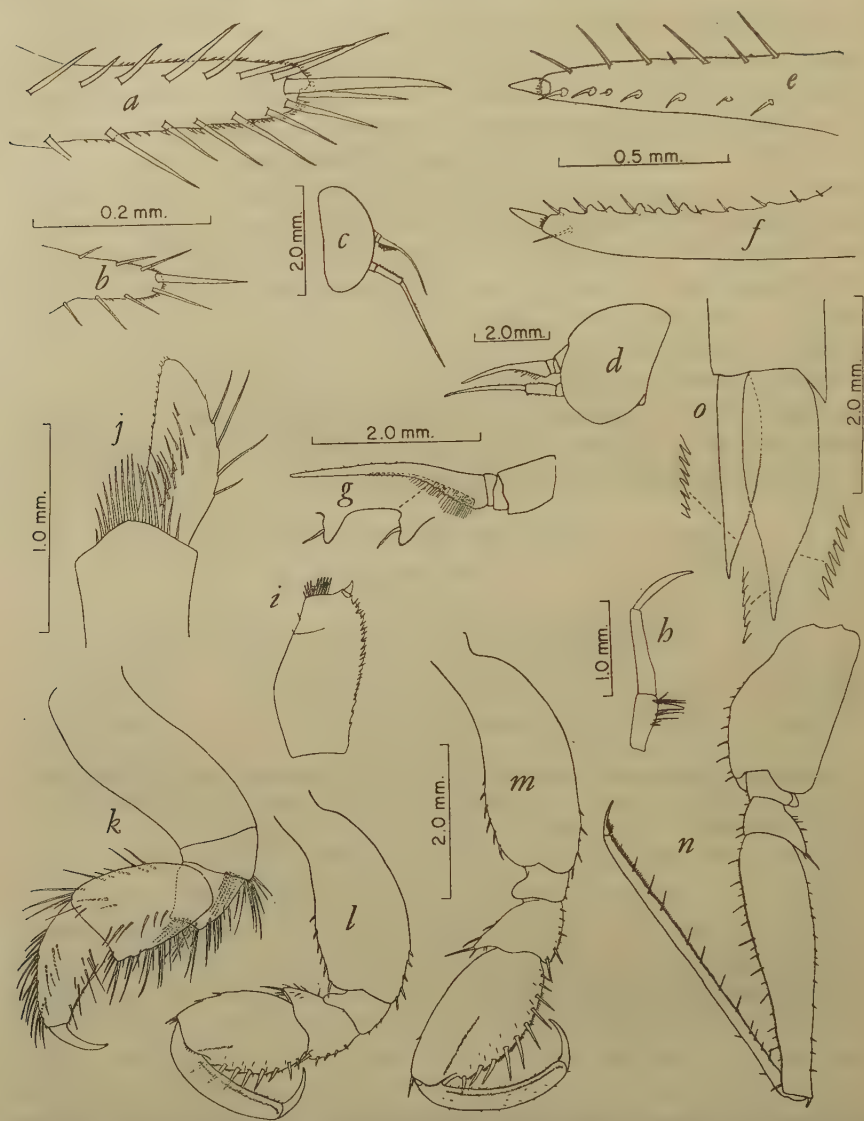

FIGURE 16.—*Parathemisto gaudichaudii* (Guérin), Gulf of Maine: *a*, Pereopod 2, carpal process, seen from above. *Parathemisto gracilipes* (Norman), west of Kyusyu, Japan: *b*, Same. *Parathemisto japonica* Bovallius, off Cape Esan, Japan: *c*, Head and antennae female. *Parathemisto libellula* (Lichtenstein), Point Barrow, Alaska: *d*, Same; *e*, pereopod 2, carpal process, seen from above; *f*, same, lateral view; *g*, antenna 1, latera view; *h*, mandibular palp; *i*, maxilla 1, palp; *j*, maxilliped, inner plate and right outer plate omitted; *k*, pereopod 1; *l*, pereopod 3; *m*, pereopod 4; *n*, pereopod 5; *o*, distal end of uropod 3. Scale same for *a–b*, *e–f*, *i–j*, and *l–m*.

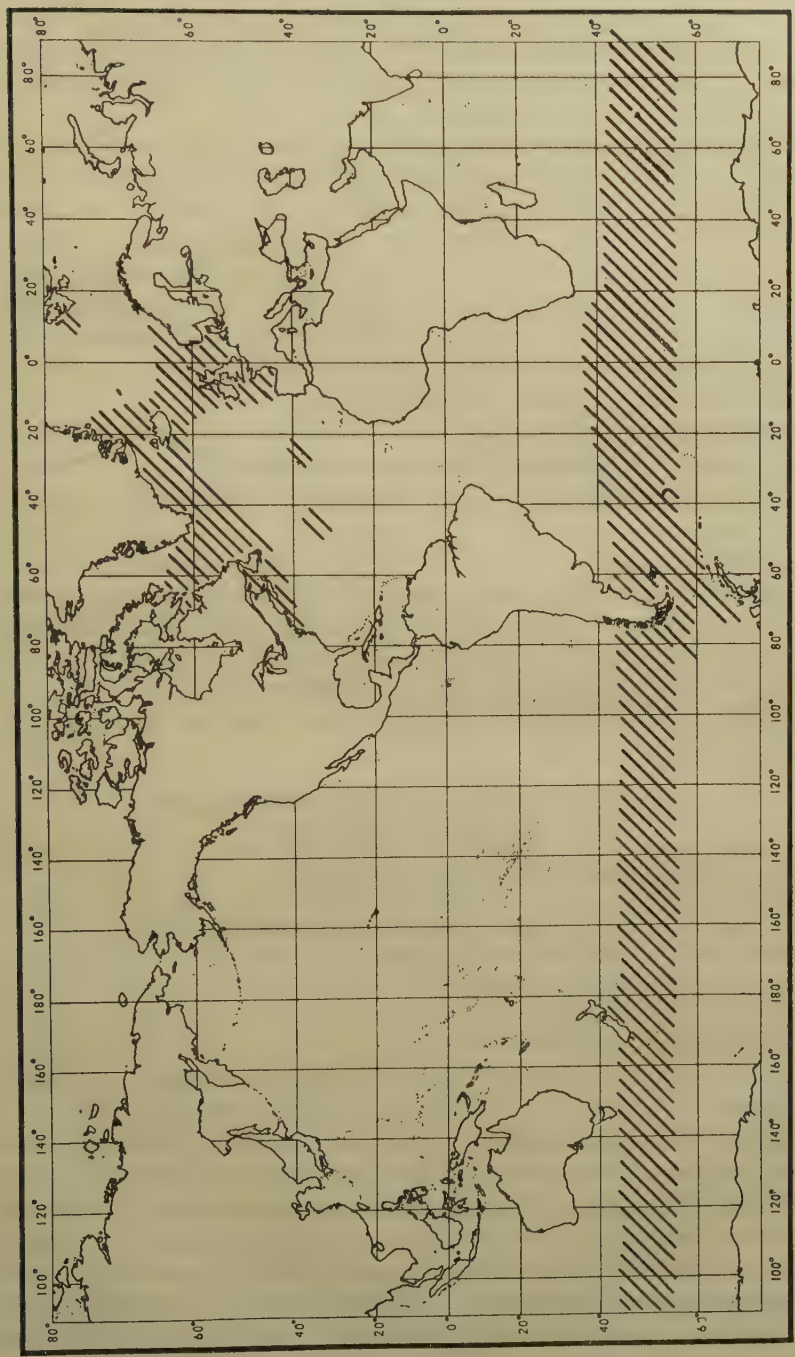

FIGURE 17.—*Parathemisto gaudichaudii* (Guérin), world distribution. The poleward limits in the southern hemisphere are uncertain.

Some care must be exercised, since Hurley observed that some female *P. gracilipes* have nearly smooth inner margins on the inner rami of uropod 3; these margins are nearly smooth in North Pacific specimens also.

According to Hurley's diagnoses, the carpal process of *P. gaudichaudii* P2 has several end spines, while that of *P. gracilipes* has one stout end spine. The carpal processes of these species are shown in figures 16*a–b*, looking down on the concave surface. Each has one large, stout spine inserted near the distal end, and a series of shorter, more slender spines distributed along the margins. The carpal process of the large specimen of *P. gaudichaudii* has about twice as many marginal spines as that of the small *P. gracilipes*, and the process is longer in relation to its breadth.

I have not seen any specimens of *P. gaudichaudii* from the North Pacific, and it is included in this paper because of the possibility, discussed under *P. gracilipes*, that Yamada's "*Parathemisto* sp. (12)" may belong here.

Distribution: As shown in figure 17, *P. gaudichaudii* is widely distributed in the cooler part of the north Atlantic with a few scattered records from warm water. Records in the southern hemisphere are less complete than in the north Atlantic, but it probably occurs throughout the Antarctic Ocean; i.e., the area between the Antarctic Continent and the Antarctic Convergence (Sverdrup, Johnson, and Fleming, 1942).

Parathemisto (Euthemisto) libellula (Lichtenstein)

Figures 16, *d–o*; 18; 19

Gammarus libellula Lichtenstein, *in* Mandt, 1822, p. 32.
Themisto libellula (Mandt), Stephensen, 1923, pp. 24–26, chart 5 [distribution].—Shoemaker, 1926, p. 4; 1955, p. 72.—Dunbar, 1946; 1957 [biology].
Euthemisto libellula (Mandt), Bovallius, 1889, pp. 281–283, pl. 12, figs. 1–31.—Sars, 1895, pp. 13–14, pl. 6, fig. 1.—Shoemaker, 1920, pp. 23–24, 28.
Parathemisto libellula (Mandt), Vinogradov, 1956, p. 211, fig. 10 [distribution].—Barnard, 1959, pp. 123, 125, pls. 22–23.

Diagnosis: The largest species of *Parathemisto*, reaching a length of 60 mm. Body segments not produced into spines dorsally. Female antennae 1 and 2 subequal; antenna 1 slender, straight, lower margin of flagellum serrate. First segment of mandibular palp setiferous. Maxilliped with distal row of long setae on basal plate and several long setae on lateral margins of outer plates. Carpal process of P2 with short end-spine and rounded lobes behind the spines on the lateral margins. P5 much longer than P6; P7 slightly shorter than P6; dactyls of P5–7 strongly pectinate at their bases. Inner ramus of uropod 3 serrate on both margins; peduncle strongly produced at inner distal corner.

Remarks: The straight antenna 1 and the produced inner distal corner of uropod 3 are characteristic of subgenus *Parathemisto*, but the elongate P5 places *P. libellula* in subgenus *Euthemisto*. The species is easily recognized by the pectinate dactyls of P5–7.

Although Mandt has always been cited as the author of this species, Mandt expressly states that the name and description were prepared by Lichtenstein. The name "*libellula*" must therefore be attributed to Lichtenstein rather than to Mandt.

Distribution (figures 18, 19): Circumpolar in the Arctic Ocean. Its distribution in the eastern part of the north Atlantic is given in detail by Stephensen (1923). He reports it from many localities near Greenland and Iceland. In the Norwegian Sea it is not found below 70° N. In the western North Atlantic the southernmost records are from the Gulf of St. Lawrence and the east coast of Newfoundland. In the Pacific Ocean Behning (1939) records it from the Bering Sea and from the Okhotsk Sea as far south as about 46° N. (southeast of Sakhalin Island). Bulycheva (1955) also reports it from the Bering and Okhotsk Seas. I have identified specimens taken in September 1958 at four stations in the vicinity of Afognak Island, Alaska, by the University of Washington M/V *Brown Bear*. No other records from the Gulf of Alaska are known to me. Vinogradov (1956) summarizes the known distributional records in his figure 10.

Aside from *P. abyssorum*, *P. libellula* was the only commonly collected amphipod in the 1950, 1951, and 1953 expeditions of the *Burton Island*. In 1950 it occurred at about one-third and in 1951 at about one-fifth of the stations occupied. The average number per station (100 m. vertical tow) was 0.66 in 1950 and 0.30 in 1951. The average number per positive station was 2.2 in 1950 and 1.5 in 1951. No correlation with variations in temperature or salinity was found.

P. libellula was taken at 5 of the 25 *Burton Island* stations in the Prince of Wales Strait in 1953. The average number per station was 1.13; the average number per positive station was 1.80.

Life history: The life history has been studied in some detail by Dunbar (1946, 1957), who points out the importance of *P. libellula* in the ecology of the eastern Canadian Arctic. It is fed on heavily by the Arctic char and especially by the ringed seal. Dunbar postulates a life cycle of 2 years, with spawning beginning in September of the second year and extending through the winter until some time in May or June. The individual is believed to breed once and then to die. If this alternating or 2-phase breeding cycle remained undisturbed, adjacent year classes would be reproductively isolated. There is evidence that a few juveniles of each year breed the following winter, so reproductive isolation of the two coexisting year classes is not complete.

All the specimens taken in the net-tow collections of the *Burton Island* were juveniles ranging in length from 4.5 to 21.5 mm. None of the females had even rudimentary oostegites. The 1950 and 1953 collections were made in August, but the 1951 collections were made from August 12 to September 21. Thus the *Burton Island* collections give no evidence for breeding in August or September, although they may not be truly representative of the *P. libellula* population. Dunbar (1957) found maturing females in ringed seal stomachs in August 1953 and July 1954, but a 2-meter stramin net hauled at 3 knots failed to collect maturing females during these months.

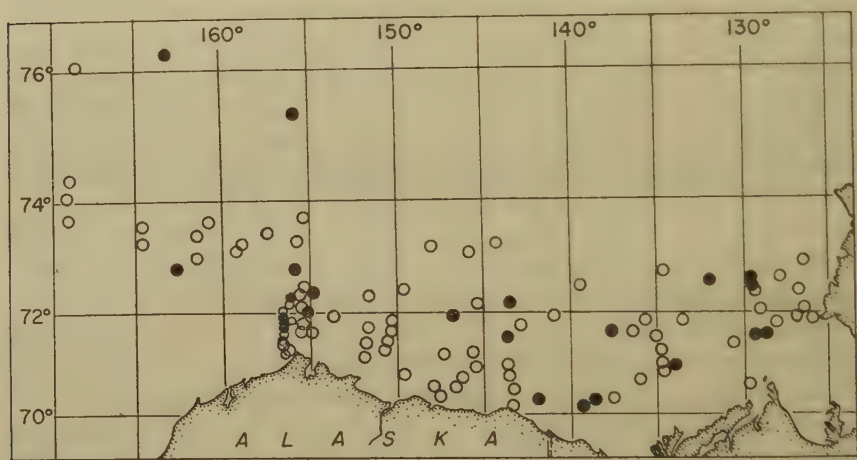

FIGURE 18.—*Parathemisto libellula* (Lichtenstein), distribution in the Chukchi and Beaufort Seas, U.S.S. *Burton Island* 1950 and 1951 cruises combined. Solid circles, positive stations; open circles, negative stations.

Shoemaker (1955) reports a collection of about 1,000 specimens washed ashore at Point Barrow, Alaska, September 12, 1949. I have examined and measured 100 specimens from this lot. They vary in length from 19 to 29 mm., with a mode of 24 mm. Most of the females have minute oostegites less than half the size of those figured by Dunbar (1957, fig. 9) to illustrate the "adolescent" female stage. The males are juveniles with segmented antennae only slightly longer than the head in the largest individuals. Some males as large as 25 mm. had unsegmented antennae. Apparently the breeding season had not arrived.

Several small lots of *P. libellula* from the Bering Sea are present in the collections of the U.S. National Museum, mostly *Albatross* collections made in early August 1893. Juveniles, adolescents, and

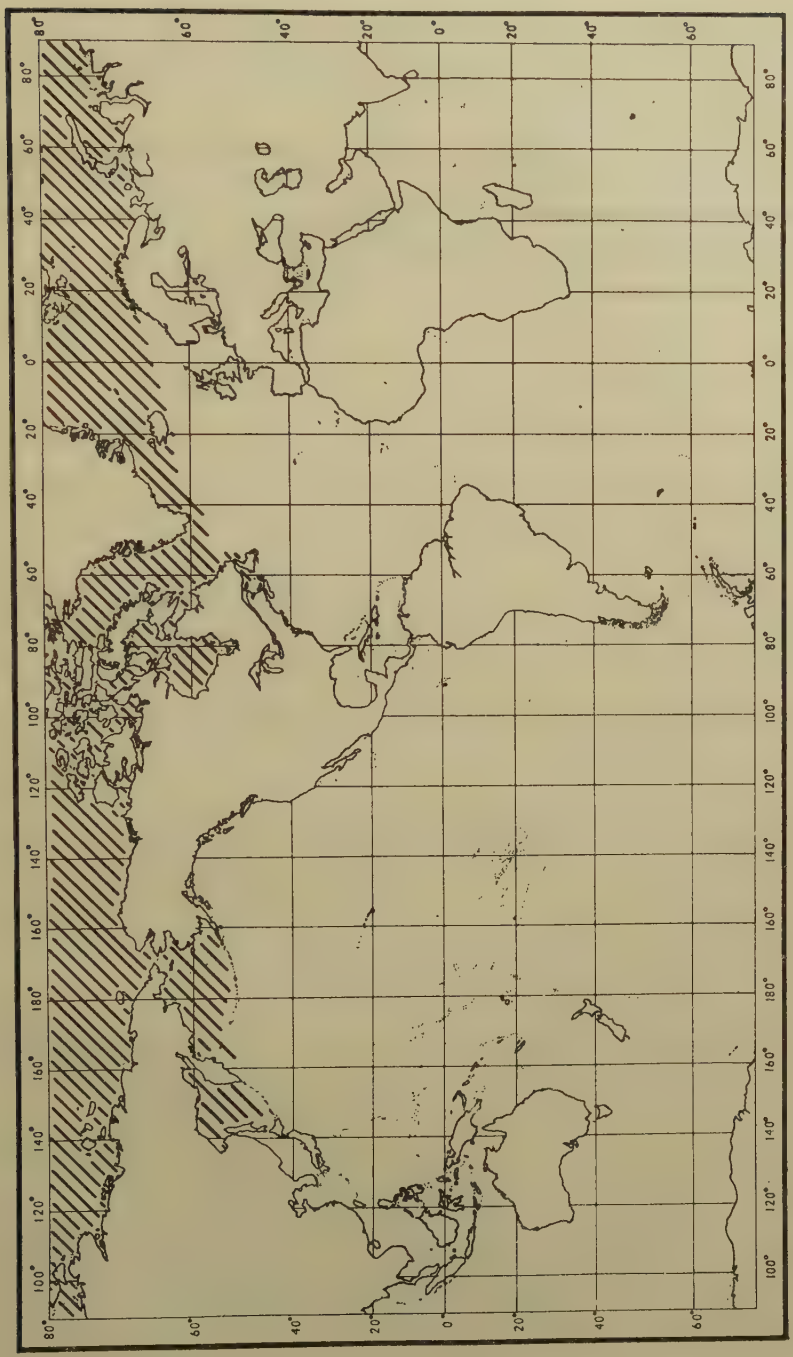

FIGURE 19.—*Parathemisto libellula* (Lichtenstein), world distribution.

maturing females are all present, and at Station 3518 (60°22′ N., 171°42′ W., August 3, 1893) an ovigerous female, 30 mm. in length, was collected. Evidently some breeding takes place during early August in the Bering Sea.

Dunbar's work on the life history of *P. libellula* and his proposed breeding cycle are of considerable interest. Much additional collecting, especially in the winter months, is needed before the validity of his conclusions can be adequately assessed.

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